

Vol. XII, Sec. C, No. 1

JANUARY, 1917

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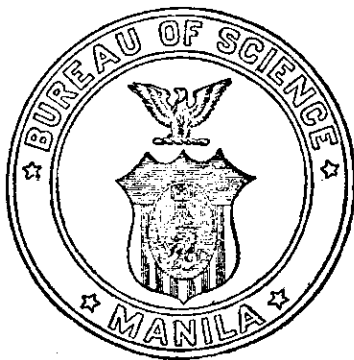
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VOLUME XII
1917

WITH 17 PLATES AND 10 TEXT FIGURES



MANILA
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DATES OF ISSUE

- No. 1, pages 1 to 72, July 17, 1917.
- No. 2, pages 73 to 116, August 14, 1917.
- No. 3, pages 117 to 176, October 16, 1917.
- No. 4, pages 177 to 248, November 9, 1917.
- No. 5, pages 249 to 316, November 9, 1917.
- No. 6, pages 317 to 391, January 28, 1918.

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THE PHILIPPINE JOURNAL OF SCIENCE

C. BOTANY

VOL. XII

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No. 1

THE APPLICATION OF PHOTOCHEMICAL TEMPERATURE COEFFICIENTS TO THE VELOCITY OF CARBON DIOXIDE ASSIMILATION

By WILLIAM H. BROWN and GEORGE W. HEISE

(From the College of Liberal Arts, University of the Philippines, and from the Bureau of Science, Manila, P. I.)

THREE TEXT FIGURES

The van't Hoff principle,¹ which states that the rate of most chemical reactions at ordinary temperatures (between 0° C. and 180° C.) is approximately doubled or trebled for each increase of 10° C. in temperature, has been applied to many processes taking place in living organisms. Its application to plant processes has been emphasized by Blackman,² while Loeb and his coworkers³ have discussed its relation to many processes in animals. Kanitz⁴ has written a monograph on the relation between temperature and life processes. We have not been able to consult this book. Denny⁵ in reviewing it says:

Consideration is given first to the effect of temperature upon the rate

¹ Van't Hoff, J. H., *Studien zur chemischen Dynamik* (revised by Cohen, E.) (1896) 129: " * * * eine Temperaturerhöhung um 10 Grad verdoppelt, resp. verdreifacht die Reaktionsgeschwindigkeit."

² Blackman, F. F., The metabolism of the plant considered as a catalytic reaction, *Science* N. S. 28 (1908) 628-636.

³ For a list of references on this subject, see Loeb, J., et al., *Science* N. S. 28 (1908) 645-648; also Kanitz, A., *Zeitschr. Elektrochemie* 13 (1913) 707, and *Zeitschr. Phys. Chem.* 70 (1910) 198.

⁴ Kanitz, A., *Temperatur und Lebensvorgänge* (1915).

⁵ Denny F. E., *Bot. Gazette* 62 (1916) 156.

of chemical processes. It is found that in general the latter follow the van't Hoff law, * * *.

Livingston and Livingston^{*} in discussing these problems make the following statement:

In much of the work that has been published on vital temperature coefficients, relatively simple physiological processes have been considered, and it seems allowable to conclude, at least tentatively, that most of the elementary chemical processes of living things go on according to the principle of van't Hoff and Arrhenius, and that such processes possess temperature coefficients, within the ordinary limits of environmental temperatures, of an order of magnitude of from about 2.0 to about 2.5. This may be regarded as a fundamental principle in physiology.

The consensus of opinion on this subject is that the principle applies only within certain limits and not at minimum and maximum temperatures for the processes concerned.

Photosynthesis is one of the plant processes that is usually cited as following the van't Hoff principle. However, since carbon dioxide assimilation is dependent on light, it is to be expected that the temperature coefficients will be similar to those of photochemical reactions, rather than to those of ordinary chemical processes. Photochemical reactions, almost without exception, have much smaller coefficients than those required by the van't Hoff principle. The ratios for the velocities of photochemical reactions for 10° intervals, given in a table by Plotnikow,⁷ are between 1.00 and 1.42. Sheppard⁸ gives a less complete list with values between 1.00 and 1.34. It is interesting to note that Weigert,⁹ in his comprehensive discussion of photochemical processes, mentions photosynthesis as one of two photochemical reactions that show unusually high coefficients.

This discrepancy appeared rather surprising and induced us to undertake a series of experiments for the further investigation of the question of the temperature coefficients of photosynthesis. The available literature, however, seemed to show so convincingly that photochemical temperature coefficients do hold for photosynthesis, that it seemed advisable to publish a discussion of the literature at the present time.

^{*} Livingston, B. E., and Livingston, G. J., Temperature coefficients in plant geography and climatology, *Bot. Gazette* 56 (1913) 349-375.

⁷ Plotnikow, J., Photochemische Studien. IV Über den photochemischen Temperaturkoeffizienten von Brom, *Zeitschr. Phys. Chem.* 78 (1911) 573.

⁸ Sheppard, S. W., Photo-chemistry (1914) 304.

⁹ Weigert, F., Die chemische Wirkung des Lichts, *Sammlung Chem. u. Chem.-Tech. Vorträge* 17 (1911-12) 183-296.

VAN AMSTEL'S WORK ON ELODEA

An attempt has been made by van Amstel¹⁰ to determine the effect of temperature on the assimilation of carbon dioxide, when light is not a limiting factor. The plant used was *Elodea*. From experiments performed at temperatures of 24° and 36° C. with various intensities of light, van Amstel concluded that increasing the light beyond 2,000 Hefner-candles had no effect on the rate of assimilation.

A series of experiments was then performed with a light intensity of 2,482 Hefner-candles and temperatures of 24°, 36.5°, 40°, 42°, and 45°. At 36.5° the injurious effects of high temperatures apparently had not set in, but they were very evident at temperatures above 40°. From the curve showing the assimilation of carbon dioxide with increasing temperatures, van Amstel obtained a value of 1.26 for the temperature coefficient between 24° and 34°.

Concerning this coefficient she says:

Now, at such temperatures for most of the physiological processes a higher temperature-coefficient is found. As a rule this even amounts to a value between 2 and 3, as in most chemical processes. By this circumstance it becomes very improbable that we really did determine the velocity of the assimilation-process itself.

Her chief reason for the above statement apparently is found in the deviation of the temperature coefficient from the van't Hoff ratio. Since, as we have shown, it is to be expected that the coefficients of photosynthesis are low, her objection fails. As a matter of fact, her experimental data show remarkably good agreement with one another, as is shown in Table I, in which we have added to the data in her summary¹¹ the corresponding temperature coefficients. In this and all succeeding determinations of temperature coefficients the following formula, given by Kanitz,¹² has been used:

$$\log Q_{10} = 10 \frac{(\log K_2 - \log K_1)}{t_2 - t_1}$$

in which

Q_{10} = temperature coefficient for an interval of 10° C.

K_2 = rate observed at temperature t_2

K_1 = rate observed at temperature t_1 .

¹⁰ Van Amstel, J. E., On the influence of temperature on the CO₂-assimilation of *Helodea canadensis*, *Rec. Trav. Bot. Néerl.* 13 (1916) 1-29.

¹¹ Op. cit. 25.

¹² Quoted by Denny, F. E., *Bot. Gazette* 62 (1916) 156.

TABLE 1.—*Velocities of assimilation of carbon dioxide at different temperatures (van Amstel, Table VI) and the corresponding temperature coefficients calculated for 10° C.*

Time of heating.	Velocity of assimilation at—			Temperature coefficient Quo.	
	24° C.	36.5° C.	40° C.	24°-36.5°	36.5°-40°
Minutes.	Milligrams oxygen per minute.				
3	200	278	293	1.30	1.16
9	200	282	306	1.31	1.26
15	200	265	303	1.25	1.46
21	200	274	285	1.23	1.11
27	200	264	246	1.25	
Average				1.23	1.25

BLACKMAN AND SMITH'S WORK ON ELODEA

Blackman and Smith¹³ have performed two experiments with *Elodea*, which are interesting in this connection. These experiments are summarized in our Table 2.

TABLE 2.—*Summary of experiments D and E of Blackman and Smith on Elodea.*

Experiment.	Initial temperature.	Final temperature.	Carbon dioxide assimilation at initial temperature.	Carbon dioxide assimilation at final temperature.
	°C.	°C.	Grams.	Grams.
D	7	21	0.0115	0.0252
E	13	21	0.0177	0.0226

In the first case the rate of assimilation was determined at 7°; then the temperature was raised to 21°, and another determination was made. The second experiment was similar to the first, the temperatures in this case being 13° and 21°. The light was the same throughout. Blackman and Smith in discussing these experiments say:

By experiment D we have established 0.0115 as the "specific temperature maximum" for the temperature of 7° C. and by E the value of 0.0177 for the temperature of 13° C.

¹³ Blackman, F. F., and Smith, A. M., Experimental researches on vegetable assimilation and respiration. IX.—On assimilation in submerged water-plants and its relation to the concentration of carbon dioxide and other factors, *Proc. Roy. Soc. London B* 83 (1910-11) 389.

From these figures the authors calculated that the coefficient of increase for 10° was 2.05. This coefficient, those calculated from van Amstel's data, and the coefficients from the experiments of Blackman and Smith are brought together in Table 3. The steady fall in the coefficients as higher temperatures are reached is similar to that usually shown by vital phenomena. However, the coefficients are much smaller than those generally shown by physiological processes. The coefficients between temperatures of 13° and 40° are within the range of those for photochemical reactions. Table 3 shows that if the results were in the form of a curve the limits within which photochemical coefficients would hold could be extended, somewhat, in both directions.

TABLE 3.—Coefficients of increase in the rate of carbon dioxide assimilation in *Elodea* with rises in temperature.

[All coefficients are calculated on the basis of a rise of 10° C.]

Range of temperature.	Coefficient.	Calculated from data of—
$^{\circ}\text{C.}$		
7-13	2.05	Blackman and Smith, p. 402.
7-21	1.75	Blackman and Smith, pp. 400, 401.
13-21	1.35	Do.
24-36.5	1.28	Van Amstel.
36.5-40	1.25	Do.

These experiments suggest that the temperature coefficients for photosynthesis in *Elodea* bear about the same relation to photochemical ratios that those of most vital phenomena do to the van't Hoff principle.

THE WORK OF KREUSLER ON RUBUS FRUTICOSUS

The work of Kreuzler has been much quoted as showing the relation between temperature and assimilation. These papers are not available. Pfeffer¹⁴ gives a curve showing the results. From this curve the coefficients for the rate of increase in assimilation have been calculated on the basis of a rise in temperature of 10° . The numbers may be slightly different from what they would have been if based on the actual figures, but they are certainly accurate enough for our purposes. The results are

¹⁴ Pfeffer, W., *Physiology of plants*, 2d ed., translated by A. J. Ewart (1900) 337.

given in Table 4. They are of the same order of magnitude as those for *Elodea*.

TABLE 4.—Coefficients of increase in the rate of carbon dioxide assimilation in *Rubus fruticosus* with rises in temperature (data of Kreuzler).

Temperature.	Assimilation.*	Temperature coefficients calculated for 10° intervals.
°C.		
2.3	4.3	
7.5	7.2	2.9
11.3	9.9	2.3
15.8	11.5	1.4
25.0	12.2	1.07
7.5-25		1.35

* Figures for assimilation were obtained by interpolation from curve, and were corrected for respiration.

The coefficients with temperatures from 11.3° to 15.5° and from 15.5° to 25° are within the limits for photochemical reactions. The coefficient for the total range from 7.5° to 25° is 1.35, which is well within the limits for photochemical processes. The coefficient for the range between 15.8° and 25° is 1.07.

According to Matthaei¹⁵ the greater part of the long and detailed investigation of Kreuzler was devoted to a single shoot of *Rubus*. A part of her discussion is as follows (p. 51):

If all the amounts of assimilation given in his paper be plotted out (fig. 1) in their chronological order, without regard to the temperatures, a curve is obtained, which is well worth detailed consideration. The general character is most decidedly that of a progressive fall in the amount of the assimilation, notwithstanding that the various temperatures occur in no particular order, but quite capriciously, and that the same temperature is often repeated. Thus, in this series, the amount of assimilation performed by the *Rubus* branch was largely a function of the time during which the experiment had lasted, and was not purely dependent on the temperature.

If this criticism is valid the work of Kreuzler indicates a coefficient near 1.0 for a much larger range of temperatures than between 15.5° and 25°. In Matthaei's curve variations in temperatures between 11° and 25° appear to have little if any effect

¹⁵ Matthaei, G. L. C., Experimental researches on vegetable assimilation and respiration, III. On the effect of temperature on carbon-dioxide assimilation, *Phil. Trans. Roy. Soc. London B* 197 (1905) 47-105.

on the assimilation, while the apparent effect of time is most marked in the latter experiments, which were with temperatures above 25° and where there is a decline in the rate of assimilation.

THE WORK OF PRJANISCHNIKOW ON TYPHA

The observation of Prjanischnikow¹⁶ that the rate of assimilation in *Typha latifolia* in direct sunlight did not change with temperatures between 9.5° and 39° C. is in harmony with the results of the experiments previously mentioned. In diffused light he found a change in rate at different temperatures. The figures are not given in the review. The results from the experiments in direct sunlight indicate a temperature coefficient of about 1.0.

THE WORK OF LUBIMENKOW

Lubimenkow¹⁷ has determined the carbon dioxide assimilation of five conifers and three deciduous trees at varying angles to direct sunlight and at temperatures of 20°, 25°, 30°, 35°, 38° C. No details concerning his method are given in the article quoted, but there are enough discrepancies in individual series to indicate that the experimental error was great. The average temperature coefficient calculated for the twenty-eight experiments for the interval 20°–30° C. was 1.4; for 25°–35° C. it was much lower.

THE WORK OF MATTHAEI ON CHERRY LAUREL

Matthaei¹⁸ made an extensive study of the relation of temperature to carbon dioxide assimilation in the leaves of cherry laurel, *Prunus laurocerasus*, garden variety *rotundifolia*; and reached the conclusion that if sufficient light and carbon dioxide were present the assimilation increased rapidly with increasing temperature between the limits –6° C. and +37° C. In a subsequent paper Blackman¹⁹ calculated that the ratio of increase in assimilation as expressed in Matthaei's curve for the 10° rise in temperature between 9° and 19° is 2.1. The statements that the van't Hoff principle applies to photosynthesis are

¹⁶ Reviewed by Batalin in *Bot. Jahresbericht* 4 (1876) 897; see also Famintzin, A., in *Ann. Sci. Nat. Bot.* VI 10 (1880) 67–80.

¹⁷ Lubimenkow, W., Variations de l'assimilation chlorophyllienne avec la lumière et la température, *Compt. Rend. Acad. Sci.* 143 (1906) 609.

¹⁸ Matthaei, G. L. C., Experimental researches on vegetable assimilation and respiration. III. On the effect of temperature on carbon-dioxide assimilation, *Phil. Trans. Roy. Soc. London B* 197 (1905) 47–105.

¹⁹ Blackman, F. F., Optima and limiting factors, *Ann. Bot.* 19 (1905) 281–295.

usually based on these figures. Kanitz²⁰ holds that Matthaei's results show a temperature coefficient approximately that of the van't Hoff principle between 0° and 37° C.

The experiments of Matthaei apparently were done with great care, and the leaf temperatures and carbon dioxide absorption were measured with a high degree of accuracy. Measurements of light were much less exact, but Matthaei believed that the amounts used in the critical experiments were great enough so that light was not a limiting factor. The sources of light were two kinds of gas burners. Her unit light intensity was a small and arbitrary one, and no measure of its actual intensity is given. In a foot note Matthaei²¹ gives the following discussion of the measurements of light:

All the intensities of light subsequently used are expressed in terms of this unit intensity by making due allowance for alterations in distance and differences in the burners employed. Of course with a compound source of light such as an incandescent mantle, such a comparison of intensities makes no pretense to accuracy, but may serve as a rough guide to the relative amounts of light necessary for maximal assimilation at various temperatures, and is absolutely necessary for convenience of reference.

It will soon also be made clear that knowledge of the exact intensity of light being used is not of critical importance in these investigations.

Some of the irregularities, which will be noted later, may be due to inexact measurements of light; but the general concordance of the results indicates that the measurements were fairly accurate. We believe, however, that errors in interpretation are responsible for the idea that the rate of assimilation increases rapidly for rises in temperature between 3° and 33° C. The rises in temperature were accompanied by increased intensities of light, and the latter factor appears to account for the changes in rate of assimilation.

The results of the experiments of Matthaei are given at the end of her paper in eleven tables.²² The first deals with respiration and the others with photosynthesis. Tables II to IV contain experiments performed with unit intensity of light and at various temperatures. Each experiment usually consisted of from three to five readings. In these, as in the other tables,

²⁰ Kanitz, A., *Über den Einfluss der Temperatur auf die Kohlendioxid-Assimilation*, *Zeitschr. Elektrochemie* 11 (1905) 689-90.

²¹ *Op. cit.* 59.

²² Since it will be necessary in this paper to make frequent reference to Matthaei's tables as well as to our own, we shall designate the former by Roman numerals, as in the original text, the latter by Arabic numerals.

the experimental data are given in full, and the results are calculated on the basis of real assimilation for 50 square centimeters of leaf and for one hour. The results of these three tables are summarized in Table 5 of the present paper, and plotted in fig. 1. The numbers from each table are plotted separately.

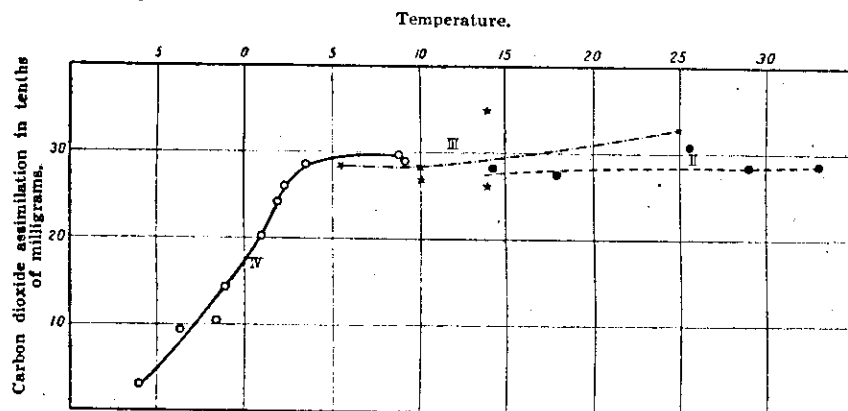


FIG. 1. Relation of carbon dioxide assimilation and temperature at unit light intensity.

TABLE 5.—Assimilation experiments at low and medium temperatures with unit intensity of light (Matthaei, Tables II-IV).

Table.	Experiment No.	Date.	Temperature.	Readings.	Average CO ₂ assimilation calculated for 50 sq. cms. and 1 hour.
		1912.	°C.		Grams.
II	V	Jan. 29	14.4	5	0.00282
	VI	Jan. 30	18.0	4	0.00274
	VII	Jan. 25	25.7	4	0.00307
	VIII	Jan. 23	29.1	4	0.00284
	IX	Feb. 1	33.1	2	0.00285
III	X	Feb. 8	5.5	3	0.00286
	XII	Feb. 7	10.1	3	0.00282
	XI	Feb. 6	10.2	3	0.00268
	XIV	Feb. 11	14.0	2	0.0026
	XIII	Feb. 5	14.2	3	0.00348
IV	XV	Feb. 10	25.0	3	0.00327
	XXI	Mar. 1	-6.0	2	0.0003
	XXII	Feb. 24	-8.6	3	0.00093
	XXIV	Feb. 17	-1.5	3	0.00105
	XXIII	Feb. 20	-1.0	3	0.00143
	XVI	Feb. 27	+1	3	0.00202
	XVII	Mar. 2	+2	3	0.00242
	XVIII	Feb. 13	+2.4	3	0.0026
	XIX	Mar. 7	3.6	3	0.00285
	XX	Mar. 4	8.8	2	0.00297
	XIX	Mar. 7	9.1	3	0.0029

The figure is similar to that given by Matthaei (p. 65) and shows that as the temperature rises from -6° to $+3^{\circ}$ there is a rapid increase in the rate of assimilation. Beyond this point the rate is increased very little if at all by higher temperatures. In regard to this part of the curve Matthaei (p. 6, par. 4) says:

Individual differences in the readings of any one series are hardly greater than the experimental error obtained in the actual experiments.

The part of the curve below 3° shows very much higher coefficients than would be called for according to the van't Hoff principle. At these temperatures many plant processes are just coming into activity. Under such conditions it would not be surprising to find that a general ratio would not hold for any particular function. The present discussion will be confined to temperatures between 3° and 33° C., where it is believed that the results of Matthaei show little or no increase in the rate of assimilation with rises in temperature.

The next series of experiments mentioned by Matthaei deal with light intensities of one, two, four, and six units with various temperatures. The details are given in Table V of her publication, and are summarized in Table VI. Her summary is copied in our Table 6.

TABLE 6.—“Summary of the experiments in Table V setting forth the ratios of the assimilation with the different intensities of light.” (Matthaei Table VI.)

Experiment No.	Date.	Temperature.	Real assimilation 50 sq. cms. in 1 hour.			
			Light intensity.			
			1.	2.	4.	6.
	1902.	$^{\circ}$ C.	Grams.	Grams.	Grams.	Grams.
XXVIII	May 3	0.4	0.00175	0.0020
XXIX	Apr. 12-13	8.8	0.00225	0.00385
XXX	Apr. 13-14	9.2	0.00205	0.00365
XXXI	Apr. 25	11.4	0.0022	0.00465	0.00505
XXXII	Apr. 26	11.4	0.0022	0.00375
XXXIII	Apr. 24-25	11.4	0.00465
XXXIV	Apr. 29	25.2	0.00215	0.00615	0.0063
XXXV	Apr. 30	25.2	0.00385
XXXVI	Apr. 19-20	24.8	0.00185	0.00485

* This figure does not appear in Matthaei's Table V.

The column for unit light intensity shows, as did the previous experiments, that with this light there was no change in the rate of assimilation with the temperatures that were above 3° C.

The rate of assimilation is much less than in the former experiments with the same intensity of light. This difference is emphasized by Matthaei and apparently is due to the time of the year, the former experiments having been performed much earlier, as will be seen from the dates given in the tables.

The column for light intensity of two units shows a higher rate of assimilation than that for one unit. There is, however, no difference in the rate for different temperatures above 0.4° .

The results with light intensity of four units are not so clear. The two determinations at 11.4° and the one at 24.8° are very similar, being respectively .00465 and .00485. The figure for 25.2° is .00615. Evidently there must be a considerable experimental error either in the result for 24.8° or for 25.2° , as a rise of 0.4° can hardly account for the difference in the results. Matthaei discards the figure for 24.8° because (footnote p. 27) the results in experiment 36 for light intensities of one and four units "are far too small in comparison with the other experiments." However, the results for one unit are well within the limits of experimental error indicated in Table I. The rates of assimilation for temperatures of 9.2° and 11.4° are also very different. It will be seen that the figure for light intensity of four units at 9.2° is less than for light intensity of two units at 8.8° . The results for light intensity of four units are plotted in fig. 2. The form of the curve seems to show that the results are such that no reliable conclusions can be drawn from them. If the figures for 11.4° and 24.8° are correct, there is very little or no rise in the rate of assimilation; if the results for 9.2° and 25.2° are reliable, there is a considerable rise. As the measurements of light were not exact, it is possible that the irregularities in the results are due to differences in the intensity of light. It will be noted that experiments 13 and 14 (Table 1) at 14.2° and 14.0° with unit light intensity show very different results. In this case, however, there are enough other experiments to show that the results are due to experimental error.

The discussion of the results with light intensities of four units is important, because it is by them that Matthaei attempts to prove that light was not a limiting factor in obtaining her result for assimilation at a temperature of 9° . The figures for light intensity of four units should be judged by their relation to the general results. In no other case will it be necessary to call into question the reliability of any figure to show that Matthaei did not eliminate the probability of light being a controlling factor at any temperature between 3° and 33° .

There were two determinations of assimilation with light in-

tensity of six units, one at 11.4° and the other at 25.2° . The figure for 25.2° is slightly higher than for 11.4° . An examination of our Table 5 will show that the percentage of increase is within the possible limits of experimental error. The coefficient for a rise of 10° as calculated from these figures is 1.17.

We will now examine Matthaei's argument more in detail.

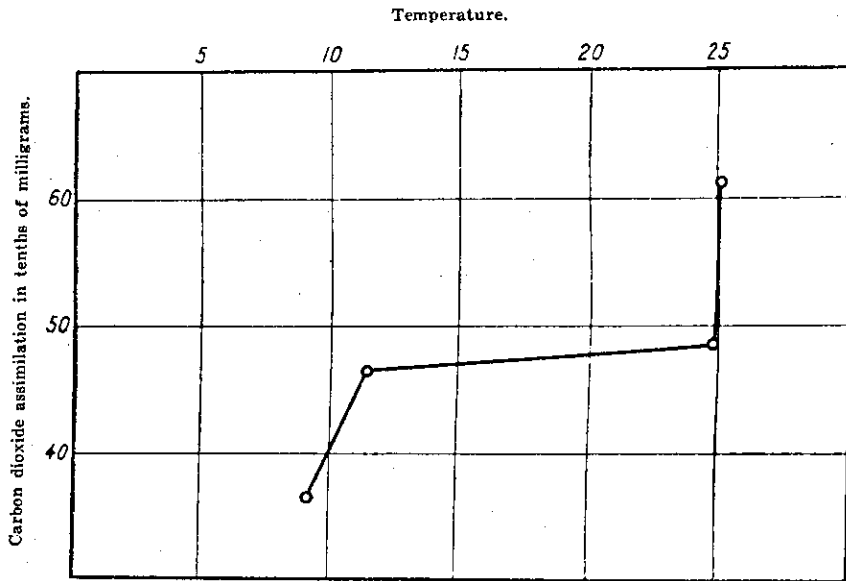


FIG. 2. Results of Matthaei with four units of light.

The following quotation ²² gives Matthaei's point of view in regard to light in her experiments:

The limiting assimilation maximum, fixed directly by any given temperature, can then only be arrived at when the light is adequate for the decomposition of the amount of CO_2 in question, and when, also, of course, that amount of CO_2 is freely available. Therefore, to reach these maxima for the higher temperatures, more light must be employed; and the evidence that is to be looked for to show that the limit is reached, and that the light really is sufficient, will be of the nature of showing that, at the given temperature, increase of light no longer augments the assimilation.

In this paper an attempt will first be made to show that in her work she has not proved that the limit was reached, and afterwards to demonstrate that the increase which she finds in the rate of assimilation is largely or entirely due to changes in the intensity of the light. Matthaei's proof that light was not a

²² Op. cit., p. 68, par. 3.

limiting factor in the critical experiments begins as follows (p. 70, par. 2) :

When the intensity is doubled, the assimilation at 0.4° C. is unaltered, but an increase is produced at the other temperatures, numbers almost identical being obtained for all of these.

The temperature is below that which we are considering. It may be said, however, that with unit intensity of light the result at 0.4° is very similar to those obtained at all higher temperatures and so is greater than would be expected from the more complete results recorded in Table 1 and plotted in fig. 1. This figure shows an increase in assimilation of considerably more than 50 per cent between 0.4° and 3.6° . Doubling the intensity of light did, however, increase this apparently too high result in Table 2 for unit intensity of light at 0.4° .

The paragraph, under discussion, continues:

When four times the light is used we find a similar phenomenon. The assimilation at 9° C. is no greater than that corresponding to twice the light, for the temperature exerts its limiting effect and the leaf can assimilate no more. At 11° C. a higher number is obtained, which, however, is not so great as that obtained at 25° C., showing that the leaf can make use of more light than is given by L. In. = 2, but it cannot use all that of L. In. = 4.

The above conclusion is reached by discarding the figure for light intensity of four units and 24.8° and regarding those at 9.2° and 25° as accurate. If the single low figure at 9.2° is not reliable, her argument fails. It has already been shown that these figures cannot be regarded as reliable enough to have positive conclusions drawn from them.

The percentage of increase between the figure for 9.2° and the one for 11.4° and four units of light is, moreover, within the possible limits of experimental error indicated in our Table 5, experiments 13 and 14. Such differences are probably not due to errors in measuring the carbon dioxide absorbed, but might well be due to variations in leaves and light. Under such conditions one experiment is certainly not a sufficient basis for conclusions.

Continuing Matthaei says:

Sixfold light gives practically the same results as fourfold light for 11° C., showing that the maximum has been attained.

If the percentage of increase is calculated it will be found that at 11.4° raising the light from one to two units, or 100 per cent, increased the assimilation 70 per cent; raising the light from

two to four units, or 100 per cent, increased the assimilation 24 per cent; raising the light from four to six units, or 50 per cent, increased the assimilation 8.6 per cent. This certainly shows that at 11° , four units is not the maximum amount of light that the leaf could use in assimilation. Nor is there any proof that the maximum was attained with six units of light, for throughout Matthaei's experiments there is for each increase in light intensity a rise in assimilation; but this is, per unit of light, progressively smaller.

In Matthaei's curve the difference in the results obtained by increasing the light from two to four units at 11° , over those caused by a rise from four to six units, is exaggerated by a misplacement of the points for these figures.

In view of the fact that four units of light are certainly not the maximum that the plant can use at 11.4° , it seems hardly reasonable to suppose that two units could have been at 9° , as is assumed to be the case by Matthaei on the basis of her apparently unreliable figures for four units.

The figures which we have just discussed for 9° and 11.4° are used by Matthaei for the lower temperatures above 0.0° in constructing her final curve. Before considering the figures for the higher temperatures, we will take up the results with light intensity of eight units. These are given in Table VII of the original publication, and are summarized in Table 7 of the present paper.

TABLE 7.—"Assimilation experiments at medium and high temperatures with light of eightfold intensity (L. In.=8). Two ordinary incandescent burners at low gas pressure." (Matthaei, Table VII.)

Experiment No.	Date.	Temperature.	Assimilation per hour per 50 sq. cms.
	1903.	$^{\circ}\text{C.}$	Grams.
XXXVII.....	Mar. 4.....	11.0	0.0072
XXXVIII.....	Jan. 29 and 30.....	25.4	0.0128
XXXIX.....	Jan. 31.....	25.3	0.0125
XL.....	Feb. 4.....	32.1	0.01295
XLI.....	Feb. 5.....	32.2	0.0130
XLII.....	Feb. 2.....	38.3	0.0115
XLIII.....	Feb. 3.....	38.3	0.0130
XLIV.....	Feb. 9.....	40.9	0.0078
XLV.....	Feb. 10.....	40.9	0.0080
XLVI.....	Feb. 6.....	42.9	0.0040
XLVII.....	Feb. 7.....	42.9	0.00355

These experiments were not used in Matthaei's final curve for assimilation at different temperatures. With the exception of the first one they were performed in the last part of January or early in February, when the leaves were more active than at the time of the experiments on which the final curve is based. Varying the temperature between 25.3° and 38.3° seems to have had no appreciable effect on the rate of assimilation. Higher temperatures were detrimental. The figure for 11.0° is lower than for temperatures between 25.4° and 38.3° . This can readily be explained as due to differences in the seasonal activity of the leaves. Matthaei (p. 83, par. 5) says:

The maximal assimilation of a leaf at 30° C. might be .0240 gramme in February, and in April be .0136 gramme, but a reduction in temperature to 11° C. would cause the same proportionate decrease in both cases.

No evidence for the correctness of the latter statement is given. There is, then, no reason for assuming, as Matthaei does, that with eightfold intensity of light there is a rise in the rate of assimilation between temperatures of 11° and 25° . These experiments, indeed, agree with all of the previous ones in which reliance can be placed, in showing that with a given intensity of light, variations in the temperature above 3° produced no appreciable effect.

We will now consider the figures for higher temperatures in Matthaei's curve. These are presented in Table XI of her publication and are summarized in Table 8 of the present paper. They are copied in greater detail than any of the previous experiments, as the figures for assimilation at 37.5° and 40.5° decrease markedly with each successive reading. The results for 37.5° will be discussed later. The still higher temperature, 40.5° , is evidently harmful and of no interest here.

The first figure is that for 15° . Matthaei's discussion of this point is as follows (p. 78, par. 7):

Experiment LVI, 15° C.—The intensity of the light employed in this experiment was thirteen times unit intensity. The lowest temperature of the bath attainable was 11° C. (that of running water at that time of year), and, in consequence, the excess of light must not be great enough to raise the temperature of the leaf more than 4° C.

Under these conditions the leaf decomposed .0070½ gramme CO_2 per hour. Now it will be seen that in Experiment XXXVII, at 11° C., the intensity of the light used was eight times unit intensity, i. e., a little more than half that available in this experiment. The amount of CO_2 decomposed per hour was, however, .0072 gramme, and therefore this leaf at 15° C. must be exposed to nearly twice the light necessary for the assimilation which it has actually performed.

TABLE 8.—Experiments showing assimilation at temperatures between 15° C. and 40° C. (Matthaei, Table XI.)

Experiment No.	Date.	Temperature.	Light intensity.	Area.	Apparent assimilation per hour.	Respiration per hour.	Real assimilation calculated for 60 sq. cm. and 1 hour.
	1903.	°C.		Sq. cm.	Grams.	Grams.	Grams.
LVI	Apr. 6	15.0	13	37.0	0.0050		
					0.0046		
					0.0050		
					0.00475		
					*0.00485	*0.00035	*0.00705
LVII	Apr. 4	23.7	26	42.0	0.0065		
					0.0080		
					0.0084		
					0.0078		
					*0.0076	*0.0009	*0.0101
LVIII	Apr. 3	30.5	46	46.0	0.0134		0.0157
					0.0116		
					0.0106		
					0.0099		
					*0.01135	*0.00115	*0.0136
LIX	Apr. 7	37.5	45	36.0	0.0154		0.0237
					0.0106		
					0.00795		
					0.0059		
					*0.0100	*0.0019	*0.0163
LX	Apr. 9	40.5	45	38.5	0.0099		0.0149
					0.0075		
					0.0060		
					0.0020		
					*0.0063	*0.0016	*0.0102

* Mean values per hour.

In Table 9 the two experiments are compared. In experiment 37 the temperature is lower and the light less intense than in experiment 56, while the assimilation is slightly greater. The difference in temperature between these two experiments would, according to Matthaei's final curve, account for an increase in assimilation from 48 to 70 milligrams of carbon dioxide. Then, according to Matthaei's argument (p. 79), if the leaf were "exposed to nearly twice the light necessary for the assimilation which it has actually performed," it was also exposed to a higher temperature than was necessary for this assimilation. Obviously, the only conclusion that can be drawn from a comparison of these experiments is that the leaf used in experiment 56, performed in April, was less active than the one used in experiment 37, done in March.

TABLE 9.—*Comparison of experiments 56 and 37 of Matthaei.*

No. of experiment.	Date.	Temperature.	Light intensity.	Assimilation.
37.....	Mar. 4	°C. 11	8	0.0072
56.....	Apr. 6	15	13	0.00705

Matthaei uses a similar argument for a temperature of 23.7° (p. 80, par. 3):

The value of the assimilation is .0101 gramme per hour, less than the amount (.0128) induced in Experiment XXXVIII., Table VII., by one-third the light. Here again, therefore, there is no doubt that we are dealing with the maximal assimilation for 23° 7 C.

Experiment 57 was performed in April, and 38 in January, when the leaves are known to be much less active. If the latter experiment is plotted with Matthaei's final curve, in which the former is used, the point for experiment 38 will be found to be considerably above the curve, showing that the argument for experiment 57 contains exactly the same fallacy as that for experiment 56.

Matthaei's reasoning in the case of a temperature of 30.5° is as follows (p. 80, par. 5):

To show that here the assimilation is maximal we must turn to the experiments in Table VIII. There the leaf chamber was in exactly the same position in the bath, the same burners were used, but were placed several millimeters further away. The value of the assimilation induced by this less intense light was, however, .0249 gramme per hour, showing that the light employed in the present experiment would have been sufficient to produce more assimilation than this, and therefore the value of .0136 gramme per hour must represent the maximal assimilation at this temperature.

Here we have a comparison between experiments performed in April and in February. The fallacy is obvious from the discussion of experiments 56 and 57.

We have seen that Matthaei has failed to show that light was not a limiting factor in any of her experiments with temperatures between 3° and 33.5°. We will now inquire into the effect of light in these experiments. In fig. 3 all of the assimilation values obtained with temperatures within the above limits, in Tables 6 and 8, are plotted with reference to light intensity. These tables contain all of the numbers used by Matthaei in plotting this part of her final curve. In fig. 3 they

The whole curve in fig. 3 is apparently the same as a curve for different light intensities at 30.5°. In Table 5 it was shown that with unit intensity of light, increasing the temperature

from 3.6° to 33.1° had no appreciable effect on assimilation. Therefore, we may assume that the value of unit intensity of light at 30.5° would be the same as in fig. 3. An examination of Table 6 indicates that this would also hold for light intensity of two units. It is probable that the intermediate points would also be the same.

Since the curve for the different light intensities at the highest temperature would, apparently, be the same as that in fig. 3, we would seem to be justified in assuming that the different rates of assimilation, shown in fig. 3, are due to changes in the intensity of the light; and that temperature was nowhere a limiting factor.

An examination of Tables 5 to 7 will show that with a constant intensity of light and temperatures above 3°, the coefficient of increase in assimilation with a rise of temperature of 10° is 1.00 or slightly more than this for the three series with unit intensity of light (fourteen experiments) in Table 5, for light intensity of eight units (six experiments between 25.3° and 38.30°) in Table 7, and for one (six experiments) and two (three experiments) units in Table 6. The two figures in Table 6 for six units give a coefficient of 1.17. The highest and lowest values for assimilation with four units in Table 6 show a coefficient of 1.38; although, as we have seen, the figures on which this is based cannot be regarded as reliable, and the coefficient probably should be lower. The above coefficients are within the range that would be expected for a photochemical reaction.

With increasing light intensities the rise in assimilation per unit of light was less and less, indicating that the reaction velocity is not directly proportional to the light intensity. That this is in agreement with the results of Pantanelli²³ on *Elodea* is very apparent, if the values are taken from his curve in Table IV.

These results are quite in keeping with those of nonvital photochemical reactions, many of which show great deviations²⁴ from a direct proportionality between light intensity and reaction velocity. Increasing the light increased the assimilation but apparently had little or no effect on the temperature coefficients. With continued increases in light intensity we apparently must reach a point where rises in the rate of assimi-

²³ Pantanelli, E., Abhängigkeit der Sauerstoffausscheidung belichteter Pflanzen von äusseren Bedingungen, *Jahrb. Wiss. Botanik* 39 (1904), 167-228.

²⁴ Weigert, F., Die chemischen Wirkungen des Lichts, *Sammlung Chem.-Techn. Vorträge* 17 (1912) 264.

lation are too slight to be measured, although, theoretically, they may occur. Reinke²⁵ and Pantanelli²⁶ both found a light intensity, about equal to direct insolation, beyond which further increases in illumination augmented assimilation very little or not at all. There is, however, no reason to believe that at such intensities the order of the temperature coefficients would be changed. The low coefficient obtained by van Amstel with light of such high intensity that further increase in illumination caused no measurable increase in assimilation is in harmony with this view. A photochemical reaction, with such intensities of light, would still be photochemical and should show photochemical coefficients. It seems reasonable to assume, therefore, that the temperature coefficients for assimilation in cherry laurel, for temperatures between 3° and 33° (and perhaps even higher temperatures), is either 1.00 or a slightly larger figure, rather than 2 or more.

Tables VIII and IX in Matthaei's publication deal with preliminary experiments in which the temperature of the leaf was not determined. These are not used by Matthaei in building her curve and are of no interest here.

Table X is headed, "An experiment with a Keith high pressure burner showing the unavoidable rise in the assimilation maximum that results, with each augmentation of the light intensity, from the decided increase of internal leaf temperature that the radiation produces, in spite of the bath temperature being kept constant throughout." The results of this table are summarized in Table 10 of the present paper.

TABLE 10.—Summary of Table X (Matthaei).

Experiment No.	Date.	Temperature.	Light intensity.	Real assimilation per hour per 50 sq. cms., in grams.
	1903.	°C.		
LV -----	Mar. 12-15 -----	18.5	18.5	0.0100
		15	9.25	0.00685
		13	4.75	0.00555
	Mar. 13 -----	13	4.75	0.0059
		11	2.87	0.0039
		11	1.47	0.0024
	Mar. 15 -----	11	1.47	0.00305
		11	0.73	0.00185

²⁵ Reinke, J., Untersuchungen über die Einwirkung des Lichtes und die Sauerstoffausscheidung der Pflanzen, *Bot. Zeit.* 41 (1883) 697.

²⁶ Pantanelli, E., *Jahrb. Wiss. Bot.* 39 (1904) 167-228.

The changes in velocity are readily explained as due to changes in the intensity of the light. When the values for assimilation are plotted with reference to light intensity they form a curve similar to that in fig. 3.

Experiment 59 (Table 8) at a temperature of 37.5° and light intensity of forty-five units, shows a marked increase in the rate of assimilation over that shown in experiment 58 with the same light and a temperature of 30.5° . Table 8 shows that the rate of assimilation at 37.5° fell off very rapidly with successive readings. This shows that at this temperature there are complicating side reactions of considerable magnitude, so that it is not to be expected that a photochemical ratio would hold. The importance of side reactions will be shown in another connection. Moreover, one experiment under extreme conditions cannot be regarded as reliable when we consider the magnitude of the experimental error with medium temperatures. For the above reasons we have thought it best not to attempt to draw any conclusion from the experiment at the temperature of 37.5° . It is interesting to note that experiments 42 and 43 (Matthaei, Table VII) with light intensity of eight units and temperature of 38.3° do not show the decrease in the rate of assimilation that is seen in experiment 59.

BLACKMAN AND MATTHAEI ON HELIANTHUS

The work of Blackman and Matthaei²⁷ has been quoted as showing a high temperature coefficient for *Helianthus*. Their statement is as follows:

For a rise of 10° , the increase with cherry-laurel is 2.1 [0.0038 at 9° and 0.0080 at 19° C.], while with *Helianthus* it is certainly bigger, perhaps 2.5, but we have not exact data yet for giving the coefficient a precise value.

The coefficient for cherry-laurel is based on Matthaei's work, which we have previously discussed. The only basis that we can find for the one for *Helianthus* is a curve (in fig. 2, p. 414) that represents the initial assimilation-maximum for *Helianthus* at different temperatures. This curve is based on four figures that they give on page 413. In Table 11 we have selected from the full experiments the data on the readings mentioned. It will be seen that the lowest temperature was obtained while it was raining and the highest with brilliant sun. It is not evident why the changes in the rate of assimilation cannot be explained as

²⁷ Blackman, F. F., and Matthaei, G. L. C., Vegetable assimilation and respiration IV. A quantitative study of carbon-dioxide assimilation and leaf-temperature in natural illumination, *Proc. Roy. Soc. London B* 76 (1905) 402-460.

due to variation in light intensity, especially since it is evident from their individual experiments that fluctuations in light intensity are accompanied by marked changes in assimilation.

TABLE 11.—*Experiments of Blackman and Matthaei on Helianthus.*

Experiment No.	Temperature.	Assimilation.	Time.	Light conditions.
	°C.		a. m.	
X	18.0	0.0090	11.30-12.00	Raining.
XI	20.8	0.0109	11.10-11.40	Cloud, haze.
	20.6			Heavy cloud.
XI	22.3	0.0131	10.40-11.10	10.48, thin cloud.
				10.52, slight rain.
				11.00, cloud, haze.
XVI	30.0	0.0290	8.5 - 9.5	Brilliant sun.

GENERAL DISCUSSION

Since carbon dioxide assimilation is effected by light, it is to be expected that the temperature coefficients should have the magnitude ascribed to photochemical, rather than that ascribed to ordinary chemical, reactions. It should be emphasized that, owing to side reactions, after effects, and other disturbing factors, the exact determination of the temperature coefficients even of comparatively simple photochemical reactions is very difficult. For example, the photobromination of toluol was first found²⁸ to have a temperature coefficient of 1.85. It has been shown,²⁹ however, that this coefficient was merely the resultant obtained from a combination of photochemical and ordinary chemical reactions, the former having a low, the latter a comparatively high, coefficient.

From the above it is evident, that with so complicated a reaction as carbon dioxide assimilation, the fact that the temperature coefficient is within the limits of photochemical coefficients over wide ranges of temperature is very significant.

A discussion of the temperature coefficient of carbon dioxide assimilation, if all disturbing factors were removed, is in the realms of speculation, but may be of interest. Plotnikow³⁰ has shown that photochemical reactions can be arranged in three groups in each of which all temperature coefficients are very similar. From this he assumes that there are in reality only

²⁸ Bruner and Czarnecky, *Bull. Acad. Sc. Cracovie* (1910) 516, quoted by Plotnikow, J., *Zeitschr. Phys. Chem.* 78 (1911) 573.

²⁹ For a discussion of this point, see Plotnikow, loc. cit.

³⁰ Loc. cit.

three photochemical coefficients; and that these are 1.04 ± 0.03 , 1.20 ± 0.03 , and 1.39 ± 0.03 .

If carbon dioxide assimilation has one of these coefficients, the work of Matthaei on cherry laurel and that of Prjanischnikow on *Typha*, in direct sunlight, would indicate that it would be 1.04. The coefficient, 1.07 from Kreuzler's work on *Rubus*, for temperatures between 15.5° and 25° , is in close agreement. The coefficients for *Elodea* are higher, but this may be due to insufficient data or complicating reactions.

Apparently, photochemical coefficients hold for lower temperatures in cherry laurel than in *Elodea*. The low temperatures at which they hold for the former plant may be connected with the fact that this plant is an evergreen and that the experiments were performed during the colder months of the year. In other words, this plant apparently is adapted to carry on photosynthesis in a normal manner at low temperatures. The following statement made by Ewart³¹ is interesting in this connection:

It appears that all evolution of oxygen ceases in tropical plants between 4° C. and 8° C., in warm temperate, subtropical, and water-plants between 0° C. and 2° C., whilst in cool temperate, arctic, and alpine plants assimilation only ceases when the plants are frozen, i. e. at a few degrees below 0° C.

A summary of the temperature coefficients of carbon dioxide assimilation calculated from the work discussed in this paper, together with the temperature ranges over which they retain the order of photochemical coefficients, is shown in Table 12. It is evident that in many cases the limits could be greatly extended in both directions, without bringing the coefficients outside the range of photochemical, much less within the range of ordinary chemical constants. We have, however, limited ourselves strictly to the temperatures for which experimental data are at hand, and in which there can be no doubt of the order of magnitude of the coefficients.

It is not surprising that carbon dioxide assimilation should show high coefficients at low temperatures, when we consider the possibility of complicating side reactions and the very high ratios shown by many physiological processes at similar temperatures. Keeping in mind the possibility of side reactions, the different methods employed by various investigators, and the corresponding experimental errors, the lack of perfect agreement in the coefficients listed above does not appear serious.

³¹ Ewart, A. J., On assimilatory inhibition in plants, *Journ. Linn. Soc. Bot.* 31 (1896) 401.

TABLE 12.—Temperature coefficients of photosynthesis, having the order of photochemical coefficients.

Range of temperature—		Coefficient.	Investigator.	Plant studied.
Studied.	In which photochemical coefficients are valid.			
°C.	°C.			
—6 to +40.5	+3 to 38.3	1.0+	Matthaei	Cherry laurel.
+7 to 21	13 to 21	1.35	Blackman and Smith	<i>Elodea</i> .
24 to 45	24 to 40	1.26	Van Amstel	Do.
2.3 to 46.4	11.3 to 25	1.16	Kreusler	<i>Rubus fruticosus</i> .
9.5 to 39	9.5 to 39	1.0+?	Prjanischnikow	<i>Typha latifolia</i> .

The coefficients that we have obtained for photosynthesis are much smaller than those for most biological phenomena, since the latter, at similar temperatures, have coefficients of the magnitude required by the van't Hoff principle. These coefficients have been so thoroughly discussed that we need not consider them here. For literature on this subject, see the introduction.

Much of the literature, including many of the minor papers on the relation of temperature to photosynthesis, is not available in Manila. Therefore, a discussion of all of the literature on the subject is impracticable and will not be attempted. The work here considered includes that usually quoted as showing the relation between temperature and the rate of carbon dioxide assimilation. The literature has been discussed in detail by Matthaei and others. Such of it as is available is of no interest in the present discussion, and the references at our disposal indicate that this is true of the remainder.

The results of our analysis of the work discussed are remarkably consistent and seem to warrant the following conclusions:

CONCLUSIONS

The results of the work on carbon dioxide assimilation, here discussed, show temperature coefficients of from 1.00 and 1.40 over long ranges of temperatures which are favorable for this process. They are much smaller than those for most vital phenomena, which at similar temperatures are generally held to be of the order of magnitude required by the van't Hoff principle.

These coefficients are of the same order of magnitude as photochemical coefficients, which is not surprising in view of the fact that carbon dioxide assimilation is effected by light.

ILLUSTRATIONS

TEXT FIGURES

- FIG. 1. Curves, showing the relation of carbon dioxide assimilation and temperature at unit light intensity.
2. Curve, showing the results of Matthaei with four units of light.
3. Curve, showing the relation of light intensity and carbon dioxide assimilation in cherry laurel.

THE ORIGIN AND DISPERSAL OF *COCOS NUCIFERA*

By O. BECCARI

(Florence, Italy)

Having had the opportunity of meeting Mr. J. F. Rock shortly after his trip to the Palmyra Islands I became much interested in his account of the exceptional conditions which he found in the flora of this small and isolated group. This flora proves, at least as far as the phanerogams are concerned, to be composed of an extraordinarily small number of species, belonging to the common strand flora of the Malay Archipelago and Polynesia, and of the coconut palm, which composes nearly the whole of the forests that cover these islands.

The Palmyra Islands belong to the category of those uninhabited coral islands, covered with dense groves of coconut palms, and of which Simmonds writes, as reported by O. F. Cook,¹ "the ungathered nuts which have fallen year after year, lie upon the ground in incredible quantities."

The special circumstances in which the Palmyra Islands are placed; their coral origin; their isolation, consequent to the great distance from any other land; the complete absence of indigenous inhabitants; the want of drinking water; the absence of any traces of economic plants that might suggest that they had ever been inhabited; and the certainty that they are but seldom visited either by fishermen or by any person who has tried to turn their wealth (which consists of the coconut solely) into a source of profit—all these give me the occasion, in addition to describing the peculiar characteristics of the coconut produced in these islands,² to offer certain considerations of an evolutionary and geographic nature, opposed to those which Mr. O. F. Cook has advanced with much competence and erudition in his two memoirs on the coconut palm.³ Cook, in effect, sustains

¹ History of the coconut palm in America, *Contr. U. S. Nat. Herb.* 14 (1910) 298.

² *Cocos nucifera* Linn. forma *palmyrensis* Becc. in Rock, J. F., Palmyra Island with a description of its flora, *College of Hawaii Bull.* 4 (1916) 1-53, t. 1-20.

³ The origin and distribution of the cocoa palm, *Contr. U. S. Nat. Herb.* 7 (1901) 257-293; and History of the coconut palm in America, *ibid.* 14 (1910) 271-342. The first of these memoirs will be denoted by "I" in this article; the second, by "II."

three principal theses, with which I entirely disagree. They are:

1. That *Cocos nucifera* must have assumed its actual specific characters upon the American continent, where it was found by Polynesian navigators, who later diffused it among their own islands, from whence it passed at a still later date into the Malay Archipelago and to the continent of Asia.

2. That *Cocos nucifera* in Asia, Malaya, and Polynesia, as in all other places where it is now found, can in no wise dispense with man's assistance and protection, without which it is incapable of maintaining its existence on the sea coasts.

3. That the ocean currents *cannot* have been efficacious means of its diffusion or be responsible for its wide distribution.

I have been the more induced to write these criticisms of Mr. Cook's assertions because this opinion of the American origin of the coconut palm appears to have found favor with several scientific authorities, among them Hugo de Vries⁴ and Geoffrey Smith.⁵

IS THE COCONUT PALM OF SOUTH AMERICAN ORIGIN?

According to the thesis so ably and fully sustained by Cook, *Cocos nucifera* cannot be of Asiatic, Polynesian, or Malayan origin, but must be "a native of South America and carried westward across the Pacific in prehistoric times;" and its "original home must be sought in some sheltered valley of the Equatorial Andes."

The old argument—and it was a very good one for holding *Cocos nucifera* to be of American origin—namely, that all the other members of the *Coccoineae* (except *Elaeis guineensis*) are American,⁶ has no longer any great weight, in view of the exceptions that recent botanical discoveries have made known.

In fact, the existence of a distinct species of *Elaeis* in Madagascar, different from *E. guineensis*, *E. madagascariensis* Beccari,⁷ and the discovery of another true *Coccoinea*, *Jubaeopsis*

⁴ Species and Varieties, etc., ed. 2, p. 82.

⁵ The Cambridge Natural History 4 (1909) Crustacea 173.

⁶ The presence in Madagascar of a species of *Elaeis* distinct from *E. guineensis*, almost induces me to suspect that the genus *Elaeis* should be regarded as being really African, and that instead of a representative having been carried from America to Africa, precisely the contrary occurred, and that the American *Elaeis melanococca* must be considered to be of African origin.

⁷ Beccari, Palma del Madagascar 55, f. 46; Contributo alla conoscenza della Palma a olio (1914) 72, t. 18.

caffra Beccari,⁸ in South Africa, must weaken the belief in a necessarily American origin of all the *Cocoinae*.

Indeed, *Jubaeopsis caffra* turns out to have many more affinities with *Cocos nucifera* than has any other palm whatever among those hitherto referred by authors to the genus *Cocos*.⁹

I have already shown elsewhere that *Cocos nucifera* is a monotypic palm, with but few affinities with the other palms included in the genus *Cocos*,¹⁰ whereas it has much in common with *Jubaeopsis*; namely, the general conformation of the fruit; the ample central cavity of the seed; and the male flowers with sepals entirely free and imbricated. This affinity to *Jubaeopsis* had led me to hazard a doubt as to whether *Cocos nucifera* may have originated, not in Polynesia or in some lands which have now disappeared from that part of the Pacific as I formerly supposed,¹¹ but rather in the islands lying in the eastern Indian Ocean or in some other lands or islands, existing in former times between Africa and India.¹² According to this hypothesis, Ceylon and the Keeling Islands must lie almost in the region where *Cocos nucifera* assumed its present specific characters. The species of *Eugeissonia*, belonging to a genus of palms peculiar to the Malay region, which until now have been referred to the *Lepidocaryeae*, I have shown to have more affinity with the *Cocoinae* than with the *Lepidocaryeae*.¹³ In the face of these

⁸ Webbia 4: 169.

⁹ After further careful study, I think it better to regard as distinct genera the subgenera *Arecastrum*, *Butia*, and *Glaziova*, proposed by me in Malpighia 5 (1888) 343. (Le Palme incluse nel genere *Cocos*). The genus *Arecastrum* is composed only of *C. Romanzoffiana* Cham., with its numerous varieties or subspecies and of the hardly specifically distinct *C. botryophora* Mart. To the genus *Butia* belong *C. capitata* Mart., and its numerous forms known by the names of *C. odorata* Barb.-Rodr., *C. pulposa* Barb.-Rodr., *C. leiospatha* Barb.-Rodr., and several others cultivated in our gardens under the names of *C. australis*, *C. campestris*, etc. The following are species of *Butia* also: *C. Yatay* Mart., *C. paraguayensis* Barb.-Rodr. (probably only a variety of *C. Yatay*), *C. eriospatha* Mart. ex Drude, and probably *C. stolonifera* Barb.-Rodr. Species of *Glaziova* are: *C. Weddelliana* Wendl., *C. coronata* Mart., *C. comosa* Mart., *C. petraea* Mart., *C. campestris* Mart., *C. flexuosa* Mart., and numerous other species described by Drude in the Flora Brasiliensis and by Barbosa-Rodriguez in his Sertum palmarum. On the whole the species of *Glaziova* amount to more than forty. *Cocos schizophylla* Mart. is *Aricuriroba Capanemae* Barb.-Rodr. (*Aricuri schizophylla* Becc.).

¹⁰ Ann. Bot. Gard. Buitenz. Suppl. 3 (1910) 795.

¹¹ Op. cit. 802.

¹² Webbia, l. c.

¹³ Webbia 4: 190.

facts the American origin of all the *Cocoinae* can no longer be considered as absolutely proved.

THE ASSOCIATION OF *BIRGUS LATRO* WITH THE COCONUT PALM

Birgus latro, the huge robber crab which is widely disseminated throughout Asiatic archipelagoes and Polynesia, is found also in the Palmyra Islands, and from Mr. Rock's account it abounds in that group along with other crustaceans. I have already made use of the association of *Birgus* with the coconut palm,¹⁴ as an argument against the suggested American origin of *Cocos nucifera*; for it seems to me to be inadmissible that *Birgus* could have been specifically evolved independently of the coconut. Without coconuts it would have nothing to live upon; whereas, if this association did not exist, the peculiar and special formation of this crab's prehensile organs—thanks to which it is able to grasp and break open the coconuts, which are its only means of subsistence, to say nothing of its climbing the trees which bear them—would surely not have come into existence. In any case, it seems to me that this association can hardly have originated in those eastern valleys of Peru wherein Cook insists that *Cocos nucifera* had its origin. It is also a noteworthy fact that *Birgus* is found in association with the coconut palm even in places far distant from each other and to which this palm might be held to have spread in a natural way, such as the Keeling Islands in the Indian Ocean and the Palmyra group in the Pacific.

I do not know if *Birgus* has been found in the Cocos Islands, in the Pacific, where however I should not be surprised if it existed; because, although the adult *Birgus* is a creature adapted to a terrestrial life, in the larval, or "zoaea," state it has a pelagic existence and, therefore, can be carried enormous distances. Nevertheless, *Birgus* seems to be absolutely unknown on the American shores of the Pacific. This gives me the opportunity to suggest the hypothesis that the long-enduring biological connection between *Birgus* and the coconut palm, which in the course of time has had the power of modifying certain organs in *Birgus*, likewise, has had the same influence in causing the coconut palm to assume some peculiar features. I allude to the extraordinary thickening of the pericarp, which from a teleological point of view has been attributed either to the advantage it gives to the fruit when floating, by which its dispersal is favored, or to the importance of deadening the shock when it falls from the tree. This second opinion is also shared by

¹⁴ Ann. Bot. Gard. Buitenz. Suppl. 3 (1910) 804.

Hugo de Vries in the work above cited. My idea is that this great development of the pericarp may be attributed to the effect of the stimulus given by the crabs during the plasmatic period to the pericarp of the young fruits, by their efforts to reach the seed, which may have caused an hypertrophy of the tissues of the pericarp itself, leading to the production of a fibrous, corklike tissue of a protective nature, such as is the bark of a tree. In consequence and by the light nature of this tissue, the fruit is made capable of floating independently of any final cause; thus some among the many fruits produced became very light, and for this cause alone their dispersal was favored in preference to that of the heavy fruits. All this, however, rests on the supposition that *Birgus* really is in the habit of climbing the coconut palm and that it does so to get at the immature fruits. In this connection I may observe that when in the Moluccas I often found imperfectly matured coconuts on the ground, which were more or less gnawed and entirely emptied of their kernels. This the natives assured me was the work of *Birgus latro*.

On the other hand Guppy¹⁵ writes that he never saw *Birgus* unhusk the coconuts given to them for food when kept in captivity, but that to keep them alive it was necessary that the nuts should be opened for them. Hence it is not perfectly certain that *Birgus* succeeds in unhusking the coconuts when these are quite ripe and have fallen in the natural course to the ground.¹⁶

It seems to me that if the nut were not free from the husk, at least partly, it would be very difficult for *Birgus* to get at the kernel of a ripe coconut in a dry state through the dense stratum of the fibrous cork-like tissue of the mesocarp; whereas, it could easily do so in a young immature fruit. This would explain why *Birgus* is forced to climb the trees to provide itself with fresh nuts; whereas, it might make use of the fallen fruits, if it could open them.

However, it is easy to suppose that *Birgus* may make use even of the fallen fruits by attacking those that are beginning to

¹⁵ Guppy, H. B., The Solomon Islands, 320.

¹⁶ The botanist who accompanied Judge Cooper on his first expedition to Palmyra Island would remark here that he has personally observed *Birgus latro* unhusking coconuts. He more than once watched it in its laborious work, tearing fiber after fiber from the nuts found on the ground. He has also found the nests of *Birgus* filled several inches thick and covering many square feet of ground with the fibers of the coconut, each fiber single. He has not observed *Birgus* climbing the trees, but on board ship a *Birgus* climbed to the top of a 100-foot mast.—J. F. Rock.

germinate; for in such cases it is possible that it might succeed in reaching the albumen by gnawing at the young sprout with its mandibles.

DID THE COCONUT PALM EXIST IN AMERICA BEFORE THE DISCOVERY
OF THAT CONTINENT BY CHRISTOPHER COLUMBUS?

Admitting that the coconut palm did exist in America on the Pacific coast before the discovery of the continent by Europeans, the data, on which Cook formed his opinion that from there it was disseminated on the Atlantic side, are so few and uncertain, that they offer little that can convince one of the correctness of his thesis. On the other hand, I cannot but wonder why the first sailors who reached that continent have not even mentioned the coconut palm, if for no other reason than because of the refreshing milk its fruit contains; whereas, there is not a sailor in the East who does not speak of the natives bringing coconuts to strangers to quench their thirst. Amerigo Vespucci, in his voyages—and he was the first who sailed along the whole length of the tropical east coast of America to the Gulf of Mexico and the Antilles—does not once tell us that the natives offered him anything of the kind. This appears very strange, since in Asia and in the Malayan islands coconuts are almost the first things offered by the natives to all new comers. I have no difficulty in admitting that Polynesians, Malaysians, or Papuans may have reached and established themselves on the Pacific shore of tropical America,¹⁷ and that they may have

¹⁷ The belief, widely accredited, that natives of Asiatic, Polynesian, or Papuan origin exist on the western coasts of Central America would appear to be confirmed also by what Amerigo Vespucci writes in the account of his first voyage [*Libro de viaggi di Amerigo Vespucci, di Stanislao Canovai: Firenze, Tipografia Tofani (1832)*]. He relates that while sailing (as it would seem) along the coasts of the Caribbean Sea, in the neighborhood of the Isthmus of Panama, he landed on an island in that sea about 15 leagues from the mainland, in which he found the most brutish and hideous people he had ever seen; he says that these savages had their mouths so full of an herb which they continually chewed that they could hardly speak. Each wore at his neck two small dry gourds, one holding the herb they were chewing, the other containing a white powder, which looked like powdered gypsum; into this one they dipped from time to time a little stick of the shape of a spindle, previously moistened in their mouths, and therewith flavored the herb they chewed with the aforesaid powder. It seems indubitable to me that such a custom corresponds to that which generally prevails among the Malays and other Asiatic populations at this day, of chewing the leaf of the betel and other things together with powdered lime, for the last must have been the white powder of which Vespucci speaks.

carried thither the coconut palm together with the banana; but I positively cannot admit that they found the coconut palm on the American shores of the Pacific, carried it back with them, and disseminated it throughout Polynesia and tropical Asia.

The difficulty brought forward by Cook, that the coconut palm could not have been introduced into America by the Spaniards or by the Portuguese, because the fruits could not have preserved their germinative faculties during so long a voyage, has no force; because, Cook's assertion to the contrary, coconuts can withstand several months' dryness, especially if kept under the influence of sea air; moreover, they can germinate while hanging in the rigging of a ship. It is exceedingly common in the Malayan islands to see a bundle of coconuts sprouting while hanging to the posts of a hut.

With respect to the origin of *Cocos nucifera* and its supposed native land among the salt-bearing regions of eastern Peru, Cook concludes by saying (II, p. 307):

"It would be reasonable to turn to these saline districts of South America if any attempts were to be made to definitely ascertain the original home of the coconut by finding it in a truly wild state." Fortunately the author hastens to add: "Such a discovery is hardly to be expected, because of the probability that localities suited to the spontaneous growth of coconuts would have attracted human inhabitants, even in very early times."

But in that case will Mr. Cook tell us why he holds that in such localities *Cocos nucifera* could have constituted itself as a specific entity, have grown, and reproduced itself, without the assistance of man, but yet not have done so on the oceanic coral islands?

And again:

We may hope, however, to find a series of local varieties or subspecies of the coconut palm in these interior localities, varieties that will be more hardy and vigorous than the maritime forms of the palm cultivated in the humid parts of the Tropics, and more likely to thrive under semi-tropical conditions.

Such a search can very well be carried out by some enterprising botanist; but, as a matter of fact, no one has met with such forms or varieties of *Cocos nucifera* in the regions mentioned. I do not claim, however, that such an event is absolutely improbable or that varieties and species of *Cocos* as yet unknown to botanists, possessing more affinity with *Cocos nucifera* than have any of the other *Coccoineae* known hitherto, may not be found in such localities; but such a find would be a less extraordinary thing than that the big fruits of the coconut palm should have crossed the Andes and thence have been dispersed among the islands of the Pacific.

DISSEMINATION OF THE COCONUT BY MARITIME AGENCY

Cook writes (I, p. 276) that the ocean currents are an effective agency for the dissemination of the coconut and that "the theory of the transfer of fruits by ocean currents has received much attention and far greater credence than the facts seem to warrant." "The poetic theory of the cocoanut palm dropping its fruit into the sea to float away to barren islands and prepare them for human habitation" is called a "time-honored fancy." (I, p. 276.) And again he says (II, p. 297): "A palm that is unable to maintain itself on the land has nothing to gain by having its nuts drifted about by the sea." It seems to me, however, that the restocking with plants of the islands in the Sunda Strait after the explosion in 1883 contradicts all these assertions, for both in Krakatau and in the small islands in its immediate vicinity that catastrophe involved the complete destruction of all organic life. This notwithstanding, Ernst² informs us that at the time of his visit to those islands, only a few years after the cataclysm, "the large number of coconut palms" was "an especially remarkable feature." In the earliest visits to the devastated islands, Doctor Treub and Professor Penzig not only picked up coconuts which had been thrown up on the beaches by the waves, but also, very soon encountered coconut palms pushing their young green fronds through the soil; and in Plate IV, fig. 7, of Ernst's book a young coconut palm at the upper edge of the tide level (southeast coast of Krakatau) can be seen; in Plate VIII, fig. 11, an entire group of coconut palms is seen "towering above the other trees;" and of this group our author writes:

"To our great delight we found the coconut palms laden with fruit. The large number of ripe nuts on the ground, *several of which had germinated and produced plants reaching one meter in height*, showed that, they must have attained the fruiting stage some years ago: a renewal of the forest is thus amply provided for. We were all refreshed by a quantity of unripe fruits which one of our Javanese companions brought down from the crowns of the palm trees." The same author on disembarking at Zwarte Hoek, likewise in Krakatau, writes: "Young coconut palms occur here and there with seedlings of *Barringtonia speciosa*, etc.;" and on page 68: "Groups of strand-plants have penetrated inland for a distance of 300-500 m." and among these are coconut palms. He adds that young coconut palms and *Pandanus* clumps are so near the edge of the sea that their stems are washed by the waves at high tide.

Another observation by Cook seems to me unsustainable; namely, that (I, p. 276) "the cocoanut palm seldom grows upon

² Ernst, A., *The New Flora of the Volcanic Island of Krakatau*, 58.

the immediate strand overhanging the water, or even in reach of ordinary waves." But everyone acquainted with the coasts of Asia and of the islands of the Malayan Archipelago and Polynesia knows the contrary to be the case. Cook himself (II, facing p. 299, Plate 54, fig. 1) gives an instructive illustration of "Coconut palms overhanging the surf at high tide, Puerto Barrios, Guatemala," and another half-tone from a photograph (fig. 2) of "Coconut palms overhanging the sea, Livingston, Guatemala." Against these assertions of Cook's one may oppose Ferguson's words:¹⁹

"The coconut tree flourishes better near the sea coast than in an inland situation. In such a vicinity it acquires more vigour, and produces with more fecundity; it never grows so luxuriant in the interior, where the air is not charged with saline particles, and salt water always seem to nourish it more than fresh water. The sea may wash the bottom of coconut trees without injury to them." And again, quoting Bertolacci, "It flourishes so very near the sea, that its roots are in many places washed by the waters without injury to the trees, until it is actually undermined."

As a result of my personal experience, also, all the arguments brought forward by Cook have not convinced me in the least that fruits of the coconut palm cannot be disseminated by the action of ocean currents, although he maintains (II, p. 324) that after his own observations no doubt can possibly remain that the contrary is the case. In fact he writes:

"For nearly two centuries the coconut has been described in books of travel and natural history, and even in formal scientific works, as an example of a plant widely distributed in nature through the agency of ocean currents." The following are also his words (II, p. 300): "The possibility that a coconut might be stranded on a newly formed island and multiply in the unoccupied soil, according to the fable, may not be absolutely excluded, but we know that the monopoly would not be of long duration." This, because the writer holds that young plants would be suffocated by "their forest-forming competitors."

I would observe, however, that these competitors on the sea shore would be only halophilous plants, which have never shown themselves to be incompatible with *Cocos nucifera*, especially on the sea beaches of coral islands, which are always in immediate contact with the sea. If on many continental and insular coasts of Asia the coconut palm is not met with, I would give among other reasons, which I shall state later, this one, that it is just because forest plants from the interior have found the means of forestalling or supplanting the strand plants which originate from drift seeds.

¹⁹ Ferguson, All About the Coconut Palm, 111.

The coconut palm (always according to Cook) "cannot be disseminated by ocean currents." He says that (I, p. 277) "it is far from correct to suppose that all nuts [of the coconut palm] which reach the water are really launched for oceanic wanderings; the chances are still hundreds to one that they will be thrown back immediately upon their own coast, like other objects floating in the surf. High waves or tides, instead of floating shore débris away, merely carry it farther inland, as everybody familiar with seacoasts knows."

That there may be some coasts the surf on which has greater power of carrying away material than of bringing it thither, I admit; but that, as a general rule, the sea does not throw back floating objects of various kinds, including the fruits and seeds of plants, is undeniable. How could all the strand floras of the world have been formed, if the sea did not carry their seeds to the beaches by means of its currents? Furthermore, suppose it were true that the surf does carry objects inland, would not that be a favorable circumstance for the dissemination of fruits which have fallen on other beaches bathed by the same sea, or into the sea itself?

THE COCONUT PALM DOES NOT ALWAYS STAND IN NEED OF THE ASSISTANCE OF MAN

Cook believes (I, p. 280) that "human assistance" is necessary to the introduction and maintenance of the coconut palm, and he says (II, p. 296) that this palm "is not known to exist except as a cultivated plant;" and (II, p. 297) that "we should find old palms surrounded by flourishing young ones growing spontaneously without the aid of man." And again, "There seems to be no authentic record of coco palms establishing and maintaining themselves on any tropical coast in a wild or truly spontaneous condition." He adds that: "The complete absence of coconuts from the extensive tropical coast line of Australia until planted by European colonists" is, "a gigantic experiment showing that the coconut did not establish itself without human help, even in a place where it afterwards thrived in cultivation." Cook (II, p. 299) also quotes Pickering²⁰ to the effect that "throughout the Pacific the coconut occurs only on those islands to which it has been carried by the natives." From another author²¹ Cook quotes: "It is to be emphasized that all coconuts are planted; the idea of a wild palm being as strange in Funafuti as that of a wild peach in England * * * I doubt whether, despite popular opinion to the contrary, a wild coconut palm can be found throughout the breadth of the Pacific."

That the assistance of man is necessary to the coconut palm is indubitable whenever it is cultivated in districts wherein there are not combined all the conditions of climate, etc., which its nature as a halophilous plant demands, and wherein it

²⁰ Pickering C., *Chronological History of Plants* (1879) 428.

²¹ Hedley, *Australian Mus. Memoir* 3 (1896) 22.

has to dispute the soil with other plants, or finds foes which injure its fruits when fallen to the ground or its young sprouting plants, or cause the death of the adult trees. But large groves of the coconut palm exist in a most flourishing condition in places where man most certainly does not contribute to their maintenance, and where they now produce themselves naturally, even supposing it were the case that the first fruits were deposited by man.

The Palmyra Islands are just such a case; there, as Darwin observed of the Keeling group, "the young and fully grown coconut trees grew intermingled with the adult plants."

It would appear that the same is the case on other coral islands of the Pacific; for examples, Palmerston Island and probably also Cocos Islands, formerly—that is, before they had been inhabited by Europeans. *Cocos nucifera* in these localities may be regarded as really wild and as a true representative of a strand flora; but admitting that the coconut palm, to establish itself on an oceanic island, has required, as a rule, the hand of man to carry its fruits thither, the case of the Palmyra Islands demonstrates that it is absolutely contrary to the truth to assert that the coconut palm can never flourish and reproduce itself spontaneously without the protection and help of man.

I cannot credit that even if the Polynesians did carry the coconut to the Palmyra Islands, they ever returned thither to take care of the plants. Yet the coconuts of the Palmyras are among the largest and finest known, and their albumen is more developed than that of most varieties cultivated by man. On oceanic islands, and especially on atolls, the coconut palm can establish itself; because when once the waves have deposited the fruits the young plants do not have to fear any competition with the primitive forest for the soil, and also because their competitors can at worst be only a few halophilous plants, produced from seeds brought thither at the same time as themselves, which can not oppose any great resistance to the growth of the coconut palm. Moreover, a most essential matter, no destructive marauders can have existed in such islands; while, on account of their great isolation, not even the foes of the coconut tree that are most to be dreaded—the red and the black beetles—have been able to reach them. Still arguing to sustain his theory, Cook writes (II, p. 303): "Unless the human friends of the young coconut are at hand to keep down the other vegetation the period of infancy is not survived." But it must be observed that the special conditions, required for the coconut palm to develop and reproduce itself independently of man, are just those found either

on newly emergent beaches, such as those of Krakatau, or on the oceanic islands on which grow only a few species of plants born from drift fruits, and on which there exists no animal likely to be hurtful.

But if one holds as correct Cook's assertion, that *Cocos nucifera* cannot have developed its actual qualities without man's protection except in America, we must admit that the cradle of mankind was America; for Cook is right when he says "that the useful cultivated plants offer the best record of man's primitive existence." If this *Cocos* cannot live without man's protection and if man must necessarily have been its distributor, we must also admit, either that man was the creator of the species *Cocos nucifera*, or that man appeared on earth at least contemporaneously with *Cocos nucifera*. The fact that the coconut palm has not established itself in Australia without help, although its nuts must certainly have been carried to its shores, can be understood when we consider that Australia is one of those regions where the conditions are precisely such that the coconut could not establish itself without man's assistance; such conditions are the predominant vegetation; the too great dryness, especially during the period of germination; and the presence of animals destructive to nuts and to young and to full-grown plants.

Cook finds another argument for maintaining that the coconut palm cannot have disseminated itself in the asserted fact that its fruits, falling from such a height, must surely be injured by the cracking of the kernel, which would have the effect of reducing "materially the chances of successful germination." But even if this were true (and in the case of some very tall palms it may perhaps happen), this must also have been the case in the birthplace of the coconut palm where there was no man ready, as he says, "to let the fruits down carefully to avoid injury" to them. Setting aside the small probability of such peril, it must be remembered that the coconut palm begins to fructify when only a few meters high; therefore, there is no danger whatever that its fruits will be injured by their fall or that there will not remain a sufficient number of them to secure the reproduction of the species.

THE CORAL ISLANDS ARE THE LOCALITY BEST ADAPTED TO THE
SPONTANEOUS REPRODUCTION OF THE COCONUT PALM

The manner in which the volcanic island of Krakatau (whence every slightest trace of vegetation was swept away by the explosion) has been restocked with plants, under our eyes, reveals the manner by which the coral islands can have been populated

with a new flora, as soon as they were in a condition to sustain a vegetation.

The transportation of seeds of plants to these coral islands may have been effected otherwise than by the usual ocean currents, by means of extraordinarily violent storms, by exceptionally high tides, and by the great waves that are occasionally produced by telluric movements, and which are of no rare occurrence in that part of the Pacific, wherein a good number of the islands appear to rest on volcanic bases.

It does not seem likely that other forces, such as the winds, or birds, or other fruit-eating animals, have contributed much to populate certain coral islands (the Palmyras amongst others) with flowering plants; because the seeds that might have been carried to them by these means belong almost wholly to species that do not tolerate the presence of salt in the soil and often not even in the air.

The oceanic coral islands of new formation can be populated only by plants of which the seeds, besides being able to float, possess also outer wrappings of such a nature that they can resist the action of salt water, and which, moreover, can tolerate the presence of salt during the period of germination; thus is explained the scanty number of plants found on oceanic islands, which, like the Keelings and the Palmyras, cannot be regarded as being the relics of ancient drowned lands.

The Palmyra Islands belong in fact, like the Keelings, to those islands constituted entirely of coral, of which Darwin wrote, as quoted by Hemsley,²² that they "at one time, must have existed as mere water-washed reefs," and to which all the terrestrial products that existed on them, before Europeans settled on them and even before any natives had reached them, "must have been transported by the waves of the sea."

It is precisely on account of this circumstance that I maintain that the coconut palm has been able to establish itself, unaided by man, both in the Palmyras and in the Keelings and, probably, in other islands, not well known to us. Indeed, it is on islands of this kind and on their scanty soil, almost level with the water, that any coconut which may have been washed up on the beach and been able to germinate, finding no hindrances nor obstacles in any preëxisting forest vegetation, would have been able to grow and prosper, because it did not find there the many enemies which would have hindered its independent development on the shores of a continent or on one of the great Asiatic islands.

²² Report of the Voyage of H. M. S. Challenger, Bot. 1 (1885), The South-Eastern Moluccas, 114.

Among the most dreaded foes of *Cocos nucifera*, the wild hogs must be reckoned. With respect to these we read in Ferguson²³ an extract from the Ceylon Examiner, as follows:

Amongst the enemies of the coconut tree the wild pig has the first place. Not only because he is the most destructive to young plantations, I suppose, but because he is about the earliest enemy that the plant has to contend against.

It is certain that on the coasts of Asia and on the shores of the Malayan and Papuan islands, where the wild pig is excessively abundant, not a single coconut would succeed in producing an adult plant without the protection of man, even though all the other conditions were favorable. There are besides the pigs other mammals such as certain rodents and herbivorous marsupials, which are very injurious to the coconut; among the last I learn that in New Guinea the "little flying opossum" (*Belidens ariel*) is in the habit of completely emptying the ripe nuts. It is noteworthy, also, that whole plantations of coconut palms can be utterly ruined by the injury caused to the adult plant by two very dangerous insects, the red beetle (*Rhynchophorus ferrugineus*) and the black beetle (*Oryctes rhinoceros*).²⁴

That the coconut palm not only can exist, but can prosper without man's help and can even produce finer and larger fruits than in places where it is carefully cultivated, is clearly evidenced by the dimensions of the coconuts of the Palmyras which I have already described. This fact may be attributed to the very special conditions inherent in the soil of the Palmyras; for though at first sight one would be inclined to think that *Cocos nucifera*, which is so exacting a plant as to fertilizing elements, could draw very little aliment from a soil composed solely of disintegrated coralline rock, of which rock the islands are formed, it does in fact find abundant nutrition therein.

The fact is that in coral islands, in addition to the detritus of various kinds, all capable of being transformed into humus, which the sea may have brought to them, the soil which forms upon them may contain fertilizing substances due to the remains of animals that have contributed to the formation of the reef;

²³ All about the Coconut, 137.

²⁴ How the presence of an insect can impede the acclimatization of a plant in a new region, the following fact demonstrates. For several years I cultivated *Aubrietia deltoidea*, a pretty *Cruciferae*, native to southern Italy, but unknown in Tuscany, which maintained and multiplied itself upon a rockery without any help, in my garden near Florence; until it was attacked one spring by the larva of a small beetle, *Ademonia tanacetii*, which devoured it to its last leaf, since which it has never reappeared.

to the accumulation of guano deposited by sea birds; and finally to the remains of the innumerable mollusks and crustaceans by which coral islands are usually populated.

THE COCONUT PALM A HALOPHILOUS PLANT PECULIARLY ADAPTED TO TROPICAL SEA COASTS AND TO OCEANIC DISPERSAL

A chemical analysis of the ashes of the coconut palm shows that all its organs contain chloride of sodium in considerable quantity; this salt, indeed, after the salts of potassium and of lime and the phosphates, being their most abundant constituent; it is even more abundant than silica, which in the state of crystals is found to be especially abundant in the leaves.

According to the summing up of Prudhomme,²⁵ a plantation of 1 hectare of the coconut palm annually draws out of the soil 120 kilograms of marine salt. And from Ferguson's report²⁶ we learn that an adult plant requires each year 1.34 kilograms of chloride of sodium. Salt, therefore, is considered an important manure for the coconut palm—far more than the quantity found in its ashes appears to demonstrate.

From the same source I learn that Doctor Gardner, to show the value that the Brasilians attribute to salt as a fertilizer for coconuts, states that "a man would walk many miles for it, pay high for a load, and then apply it to a single tree." Elsewhere, it is stated that sea weeds and the ashes of plants that contain much salt are used as manures for the coconut palm. Ferguson also states (p. 142) that the Singhalese "invariably throw a little salt into the holes before they place the coconut plants in them." And on page 111, speaking of a new plantation of coconuts which is being made inland and at a distance from the sea, he says: "it is customary to throw a considerable quantity, as much as half a bushel, of salt into the hole which receives the coconuts."

Prudhomme,²⁷ writing of the toleration of the coconut palm for marine salt, asks if marine salt should not be reckoned among the fertilizers to be administered to this palm, as it seemed to him, that instead of merely tolerating it, the coconut had a real preference for this salt. The excessive toxicity of sodium chloride for plants is well known; the coconut palm, however, is one of the few that can live on a salt soil. For that reason I am not able to understand how a plant endowed with

²⁵ *Le Cocotier*, 262.

²⁶ *Op. cit.* 66.

²⁷ *Le Cocotier*, 40.

such high hereditary halophitism—which, therefore, not only tolerates, but actually prefers, a salt soil and, moreover bears fruit so constituted as to be, as Seeman writes,²⁸ “often tossed about the ocean for months without losing its germinating power from the effects of salt water”—can have been plasmated or brought into existence in a region remote from the sea.

That *Cocos nucifera* is a true halophyte, that is to say, a plant capable of resisting the physiological action of mediums rich in chloride of sodium and in the other salts that are characteristic of sea water, the very presence of which is pernicious to most other types of vegetation, shows that it must have been placed in close contact with salt soils during the period of its evolution; considering, therefore, all the other circumstances that may have been required during and for the evolution and plasmation of the species *Cocos nucifera*, we are led to conclude that it must have originated on maritime shores.

Few are the true halophytes, and for this reason the flora of maritime shores and of the coral islands is poor in species, but in compensation they are of extremely wide geographic distribution. And this is because there are few plants having seeds tolerant of salt and at the same time provided with fruits capable of floating and of enduring a long immersion in salt water and, hence, fitted for long voyages. The coconut palm is one of these few. It is true that this palm can grow and even prosper far from the sea and can exist at a certain elevation above it, but it is probable that in these localities it can always find the quantity of chloride of sodium it needs. But although it is true that the coconut palm is capable of adapting itself to non-saline soils, as other halophilous plants can do, it none the less remains true that if *Cocos nucifera* were not a plant of the sea shore, and therefore an indubitable hereditary halophyte, it would not be better suited by a soil rich in chloride of sodium than by a soil devoid of that salt. It was therefore on the shores of the sea and especially on those of the coral islands that *Cocos nucifera* must have found the conditions under which it assumed its present specific characters; because there it would have had little to fear from the competition of other large plants of the strand flora and because there, also, it had not to struggle against powerful foes. Therefore, it cannot be admitted that the coconut palm is “unable to maintain itself on the sea coasts,” and “the popular idea” that the “coconut palm is a plant specially adapted to tropical sea coasts” is, and remains, a true idea.

²⁸ Fl. Vit. 276.

CONCLUSIONS

From the preceding study, which was chiefly suggested to me by the conditions in which the Palmyra Islands were found by their explorers, Messrs. H. E. Cooper and J. F. Rock, I conclude:

1. That the coconut palm may have been very easily disseminated by the agency of oceanic currents.
2. That the coconut palm is a halophilous plant with a predilection for the sea shore.
3. That an Asiatic or Polynesian origin of the coconut palm is more probable than an American one.
4. That the coconut palm can occasionally exist and reproduce itself in the tropics independently of man, and that the latter's protection is necessary to it only when it occurs in regions wherein its existence is disputed by the nature of the soil, by other preëxisting vegetation, or by foes of various kinds.

NEW SPECIES AND A NEW GENUS OF BORNEO FERNS,
CHIEFLY FROM THE KINABALU COLLECTIONS OF
MRS. CLEMENS AND MR. TOPPING

By EDWIN BINGHAM COPELAND

(From the College of Agriculture, University of the Philippines,
Los Baños, P. I.)

TRICHOMANES Linnaeus

TRICHOMANES BROOKSII sp. nov.

Gonocormus; rhizomate filiforme late repente nigro, pilis castaneis minutissimis vestito; stipite 5 ad 20 mm alto, filiforme, erecto, fere nigro, nudo vel sparsissime pubescente, haud alato; fronde usque ad 4 cm alta et 25 mm lata, pseudotripinnatifida, rhachi alata; segmentis infimis fere oppositis ca. 2 cm longis maximis, adscendentibus, parte mediale sympodiale, pseudopinnatifida vel -bipinnatifida; segmentis ultimis obtusis vel acutis, univerviis, venulis falsis carentibus; indusio profunde campanulato, late alato indeque in apice segmenti dilatati immerso, ore patente vix bilabiato, receptaculo exserto.

Sarawak, Mount Bongo, *Brooks and Hewitt*, 1908.

By the description, this appears to be near to *Trichomanes Hosei* Baker, of Mount Matang, which, however, seems to be typically pinnate in plan, with much more narrowly winged and rather two-lipped involucres. Above the forking of the veins of *Trichomanes Brooksii*, they are connected for a notable distance by the lamina, which thus becomes conspicuously widened at these points.

HYMENOPHYLLUM Smith

HYMENOPHYLLUM FOXWORTHYI sp. nov.

Euhymenophyllum H. blumeano affine, involucro fere omnino immerso; rhizomate filiforme, late repente, sparse fusco-piloso; stipite ca. 3 cm alto, filiforme, ad apicem ipsum plerumque anguste alato; fronde 5 ad 8 cm alta, 12 ad 20 mm lata, utrinque angustata, primo sparse pilosa, mox glabrescente, olivacea, fuscescente, rhachi anguste alata; "pinnis" pinnatifidis, "pinnulis" paucis, maximis furcatis, segmentis integris, 1 mm latis, planis, acutis obtusis vel marginatis, costis applanatis, parietibus cellularum crassis, pariete marginale segmenti valde incrassata,

uniforme (haud intus crenulata), cellulis marginalibus et costas secus opacis; soris segmenta prima acroscopica terminantibus, involucre anguste obconico immerso, limbo bilabiato libero brevissimo, late rotundato, subintegro, receptaculo clavato, breviter exserto.

Sarawak, Mount Santubong, *Foxworthy* 458, June, 1908.

Clearly distinguished by the opaque margin and *Trichomanes*-like sorus. The former is distinct in character from that of *Crepidomanes*; and in spite of the latter, I believe there is no doubt as to the affinity and proper classification of the plant.

HYMENOPHYLLUM CLEMENSIAE sp. nov.

Euhymenophyllum minutum pilosum; rhizomate filiforme glabrescente; stipitibus usque ad 1 cm longis, aut alatis usque ad pedes, aut fere omnino exalatis; fronde usque ad 3 cm alta, 1.5 cm lata, utrinque angustata, fusciscente, ad alam latam pinnatifida; segmentis obtusis pinnatifide vel dichotome incisis, segmentis ultimis integris, oblongis, obtusis, 0.7 mm latis, costis pilosis, pilis fuscis, simplicibus, subdeciduis, cellulis laminae minutis, uniformibus; soris ad vel ultra medium indusium immersis, parte immersa dense sed subdecidue pilosa non carinata, labiis liberis semiorbicularibus glabris, receptaculo clavato incluso vel breviter exserto.

Mount Kinabalu, Gurulau Spur, *Mrs. Clemens* 10780 (type), *Topping* 1619; *Kiau, Mrs. Clemens* 10226.

Clearly distinguished in its subgenus by the long, simple hairs on the veins, particularly dense hairiness of the lower part of the involucre, and glabrous lips. The color and pubescence place it in the group of *Euhymenophyllum* which approaches *Leptocionium*.

HYMENOPHYLLUM HOSEI sp. nov.

Leptocionium lamina plana, rhachi late alata; rhizomate crasso-filiforme, glabrescente, laete fusco; stipite 10 ad 17 mm alto, fere ad basin alato; fronde 4 ad 5 cm alta, 2 ad 3 cm lata, ovata, bitri-pinnatifida, rhachi nigro-fusca, ubique late alata ala denticulis sparsis ornata; pinnis inframedialibus majoribus, ad alam rhachidium ipsarum pinnatifidis, pinnulis superioribus simplicibus, inferioribus furcatis vel rarius pinnatifidis cum 3 ad 5 segmentis; segmentis 2 ad 3 mm longis, 0.8 mm latis, obtusis, ubique anguste denticulatis, marginibus et dentibus nigrescentibus, lamina alibi fusciscente; soris in segmenta prima acroscopica pinnarum superiorum insertis, parte inferiore obconica immersa, receptaculo crasso-setiforme, labiis fere aequilongo, involucre extus deorsum denticulato vel aspero vel fere nudo, ca. ad medium fisso, labiis ovatis inconspicue dentatis.

Sarawak, Mount Trekan, altitude 600 meters, *Hose 730*, 1894-95.

Distinguished from otherwise similar species by the broad, flat wing of the rachis. The blackish margin is occasionally found in other species and may not be a constant character.

HYMENOPHYLLUM PERFISSUM sp. nov.

Leptocionium lamina plana, involucro fere ad basin fisso labiis integris; rhizomate filiforme, fusco-nigro, ramoso, nudo; stipite 10 ad 15 mm alto, glabro, filiforme; fronde ca. 4 cm alta, 10 ad 15 mm lata, glabra, pinnata, rhachi sursum anguste alata ala integra, deorsum vix marginata; pinnis majoribus subpinnatifidis segmentis 3 ad 5, minoribus furcatis, minimis simplicibus, segmentis ca. 4 mm longis, vix 1.5 mm latis, obtusis, serratis dentibus paucis subspiniformibus, fuscis vel fusco-olivaceis; soris segmenta abbreviata prima acroscopica pinnarum subapicalium occupantibus, receptaculo fusiforme incluso, involucro $\frac{5}{8}$ ad basin fisso, labiis obovato-orbicularibus, integris, nudis, 1.5 mm longis.

Mount Kinabalu, altitude 3,700 meters, on tree trunks, *Mrs. Clemens 10588*.

Apparently a quite distinct little plant.

PTERIS Linnaeus

PTERIS CLEMENSIAE sp. nov.

Species gregis *P. quadriaurita* sensu latiss., pinnis infimis non furcatis; stipitibus 30 ad 50 cm altis, fuscis, ad basin paleis castaneis vestitis, alibi sub lente minute punctulatis; fronde ca. 45 cm alta, 40 cm lata, pinnata, parte apicale 25 cm longa; pinnis 2- vel 3-paribus, infimis paullo maximis, petiolulis ca. 1 cm longis, lanceolatis, ca. 25 cm longis, 7.5 cm latis, in caudam angustissimam fere 4 cm longam terminantibus, ad alam 0.2 ad 0.4 mm latam pectinatis; costa inferne straminea prominente, superne angustissime bialata, alis ad insertionem costulae quaeque in spinulam excurrentibus; segmentis usque ad 4 cm longis, 5 ad 6 mm latis, supra mediam 2 ad 3 mm distantibus, obtusis vel minute et obscure mucronulatis, venis utroque latere usque ad 24 prope costulam furcatis et 6 simplicibus; indusio griseo, 0.6 mm lato, fere ad sinum et apicem attingente.

Mount Kinabalu, near Lobang, *Mrs. Clemens 10348* (type), *Topping 1602*.

PTERIS TOPPINGII sp. nov.

Stipite 40 cm alto, glabro, stramineo-viride; fronde 30 cm alta, parte apicale 20 cm alta, 7 cm lata; pinnis utroque latere 2 vel 3, infimis brevipedicellatis (petiolulis 2 mm longis), sequentibus sessilibus, infimis ca. 20 cm longis, in segmenta 3 ad 4 cm longa, 8 mm lata terminantibus, ad alam fere 1 mm latam pinnatifidis;

costa inferne prominente fusca, superne canaliculata, non spinifera; segmentis ubique contiguis vel imbricatis, 3 ad 4 cm longis, 1 cm latis, apice late rotundatis, integris, atroviridibus; venis utroque latere ca. 14 fere ad costulam furcatis et 3 simplicibus, omnibus inconspicuis; indusio angusto (0.6 mm lato), soro aperto ultra 1 mm lato.

Mount Kinabalu, Khota Balud to Kibayo, *Topping 1488*.

A species clearly distinguished by its broad and close segments.

PTERIS PURPUREORHACHIS sp. nov.

Species gregis *P. longipinnulae*, stipite rhachique atropurpureis; stipite 30 ad 40 cm alto, basi paleis parvis pallidioribus praedito, sursum glabro, nitido; fronde 40 cm alta, deltoidea, parte apicale 20 cm alta; pinnis utroque latere 3- vel 4-paribus, stipitulatis sed petiolulis alatis, infimis furcatis, 20 ad 25 cm longis, acuminatis, ad alam 3 ad 4 mm latam pinnatifidis; costa superne subbialata, spinulis ad insertiones costularum appressis; segmentis fertilibus 7 ad 8 mm, sterilibus usque ad 1 cm latis, 3 vel 3.5 ad 5 cm longis, obtusis vel acutis, inter se 2 ad 5 mm distantibus, apices versus serrulatis, membranaceis; venis infimis plerumque bifurcatis, aut liberis aut more *P. biauritae* anastomosantibus et areolam unam costalem includentibus, sequentibus furcatis vel rarius bifurcatis usque ad 14-paribus, simplicibus ca. 3; soro sinum interdum transeunte, apice remoto, indusio pallido, 0.8 ad 1.0 mm lato.

Mount Kinabalu, Lobang, *Mrs. Clemens 10350* (type), *Topping 1790*.

HUMATA Cavanilles

HUMATA KINABALUENSIS sp. nov.

Euhumata, *H. repenti* et *H. alpinae* affinis, perfectius dimorpha et dentium carentibus; rhizomate generis typicale, paleis magnis persistentibus, marginibus earum pallidis; stipitibus frondium sterilium 2 ad 3 cm, frondium fertile 4 ad 5 cm altis, sparse squamosis; fronde sterile ca. 6 cm alta, 5 cm lata vel minore, pinnata, rhachi valida, pinnis infimis ad costam complanatam pinnatisectis, segmento infimo basiscopico pinnatilobato, pinnis sequentibus incisis, segmentis oblongis vel obovatis, obscure serrulatis, obtusis, coriaceis, deorsum et inferne squamatis; fronde fertile aequale vel longiore, lamina valde angustata; soris magnis in lobos truncatos breves apicalibus, indusio quam alto latiore.

Mount Kinabalu, below Paka Cave, *Topping 1745*.

The sori are impressed on the fertile tooth, so as to produce swellings on the upper surface.

NEPHROLEPIS Smith

NEPHROLEPIS (?) MARGINALIS Copel. sp. nov.

Stipite 45 cm alto, badio, pilis brevibus vestito; fronde 70 cm alta haud deorsum angustata, pinnata, pinna apicale elongata, rhachi et praecipue deorsum costis minute velutinis; pinnis rectis, infimis 18 cm longis, 13 mm latis, brevi-stipitatis, obtusis, auriculis brevibus praeditis, crenulatis, papyraceis, glabris, superne nigris (in herbario), inferne atroviridibus; venis furcatis; soris marginalibus vel submarginalibus, contiguis; indusiis 0.8 mm latis, 0.4 mm altis, basibus adnatis late rotundatis, apicibus truncatis.

Mount Kinabalu, Gurulau Spur, *Topping 1632*.

The specimen is incomplete, being without caudex. By the characters of the sorus, the plant is a *Cystodium*, and I feel sure the affinity thus suggested is a real one. The phylogeny of *Nephrolepis* has never been cleared up, and I believe that this species furnishes the necessary clue to it, the line being *Dicksonia-Cystodium-Nephrolepis*. We have, therefore, to go back to *Dicksonia*, commonly treated as outside the *Polypodiaceae*, to find the common ancestor of *Nephrolepis*, of the *Balantium* series (*Saccoloma*), and the very extensive series of *Dennstaedtia* derivatives. To find an ancestor common to these ferns and the other *Polypodiaceae*, we must of course go still farther back. To establish natural families, we have therefore either to include *Cyatheaceae* and *Matoniaceae*, and perhaps still other of the recognized families, in the *Polypodiaceae*, or else to split *Polypodiaceae* into the several phylogetic series. If the latter alternative is tried, the resulting groups will defy definition.

CYATHEA Smith

CYATHEA CAPITATA sp. nov.

Caudice 3 m alto; stipite 25 cm alto, 1 cm crasso, deorsum nigro paleis stramineis 15 mm longis 3 mm latis valde acuminatis integris vestito, sursum sordide atropurpureo, glabrescente; fronde 1.5 ad 2 m longa, utrinque angustata, abrupte brevi-acuminata, rhachi purpureo-fusca, segmento apicale deltoideo, basi lobato; pinnis subsessilibus, basi aequaliter truncatis, apices serratos versus sensim angustatis, alibi integris, potius acuminatis quam caudatis, glabris, papyraceis, inframedialibus 18 cm longis, 3 cm latis, horizontalibus; venis conspicuis, 2- ad 4-furcatis, venulis soriferis plerumque super soros anastomosantibus; soris in lineam unam irregularem utroque latere costae et ca. 5 mm distante instructis; indusio laete fusco nitido, tenue sed persistente.

Mount Kinabalu, Marai-parai Spur, *Mrs. Clemens 11033*.

An exceedingly well-marked species of the group of *Cyathea Brunonis*, from which it differs in the stout stipe and rachis of darker color, less scattered sori, anastomosing veins and wholly distinct apex. The anastomosis of the veins, as a feature correlated with broad, entire laminae of

frond or pinna, duplicates conditions already familiar in many other genera, *Athyrium*, *Dryopteris*, *Polypodium*, etc.

Cyathea Brunonis Wall. has of late been treated as identical with *C. moluccana* R. Br.; this may be proper, but with five or six Bornean species in the group, distinguished now by the apex of the frond, now by the base of the stipe, I would want to compare complete specimens, rather than very imperfect descriptions, before I believe it. I do not know *Cyathea moluccana* at all, but have in hand four sheets of *Cuming* 378, cited by Hooker with the description of *C. Brunonis*.

CYATHEA PSEUDOBRUNONIS sp. nov.

Fragmentum solum a C. J. Brooks ad Bidi in Sarawak anno 1907 lectum et sub nomine *C. Brunonis* sine numero distributum adest; qua specie rhachi validiore, pinnis longioribus, marginibus plus parallelis ubique crenato-sinuatis, textura crassiore, venis simplicibus multis, et praecipue indusiis nullis vel mox fugacibus distinguendum est. Rhachi castanea glabrescente; pinnis brevistipitatis, basi superiore truncatis inferiore truncato-cuneatis, ca. 30 cm longis, 3 cm latis; soris irregulariter 3-seriatis, ad venas simplices plerumque carentibus.

The main veins are notably stout, with usually four, less frequently three or five branches; and between them are usually two simple veins, leaving the costa near the main veins or at any points between them. There are no entire sori on my specimen, but many from which few sporangia have been shed; and no trace of an indusium can be detected. On Cuming's specimens of *Cyathea Brunonis*, collected about eighty years ago, the indusium can be seen a meter away with the naked eye, though the sporangia of many sori are entirely gone.

CYATHEA FUSCOPALEATA sp. nov.

Verosimiliter arborescens, sed caudice ignoto; stipite 75 cm alto, parte inferiore 20 cm longa paleis linearibus 1 ad 2.5 cm longis fuscis minute ciliatis dense vestita, sursum rhachique fusco-stramineis, glabris; fronde 75 ad 100 cm alta, 35 ad 45 cm lata, pinnata, pinna apicale aliis simile, minore; stipitulis pinnarum 3 ad 10 mm longis, basibus nigro-fuscis ad rhachin articulatis; pinnis majoribus inferioribus 16 ad 22 cm longis, 25 ad 35 mm latis, anguste lanceolatis, basi rotundatis vel interdum rotundato-cuneatis, apice acuminatis, rectis vel falcatis, apices versus serratis, alibi integris, subcoriaceis, glabris; venis 1 ad 3 furcatis, inter eas 0-2 simplicibus, proximis, liberis; soris 1-ad 3-seriatis, costae approximatis, exindusiatis.

Sarawak, Siol, native collector 2503, February-June, 1914.

Other collections probably representing this species, but without the base of the stipe, are 2657 from Mount Merinjak, and 1568, without stated locality; No. 68, the frond of a young plant, cannot now be determined to the species.

This is perhaps nearest to *Cyathea articulata*, from which it differs in the narrower pinnae and closer venation and sori, as well as in the paleae.

CYATHEA KINABALUENSIS sp. nov.

Caudice erecto haud arborescente; stipite 75 cm alto vel altiore, deorsum atro-castaneo, ad pedem paleis rufo-stramineis anguste linearibus ciliatis 2 ad 2.5 cm longis dense vestito, sursum rhachique fuscis vel castaneis glabris vel minute et sparsissime squamulatis; fronde 75 cm alta vel multo altiore; pinna apicale aliis simile; stipitulis pinnarum 5 ad 20 mm longis; pinnis majoribus inferioribus usque ad 25 cm longis et 4 cm latis, basi rotundatis vel oblique cuneatis, apicibus acuminatis vel caudatis, rectis vel falcatis, praecipue apices versus serratis, papyraceis, glabris; venis plerisque 3-furcatis et sine venis simplicibus interpositis; soris plerisque irregulariter biseriatis, a costa remotis, exindusiatis.

Mount Kinabalu, Gurulau Spur, Mrs. Clemens 10840 (type), 10861, Topping 1634.

Most nearly related to *Cyathea arthropoda*, from which it differs in its darker axes and relatively narrower pinnae with more nearly parallel sides, as well as in the long paleae.

Whoever is disposed to rename some of these species in *Alsophila* should have difficulty in overlooking the fact that they are nearly related to *Cyathea Brunonis* and *C. capitata*, but not at all nearly so to *C. extensa* (Forst.) Swt.

CYATHEA TOPPINGII sp. nov.

Rhachi fusco-purpurea, sub lente minute furfuracea; pinnis stipitulatis, sterile 35 cm longa, 9 cm lata, rhachi atropurpurea, superne velutina, alibi glabra vel glabrescente; pinnulis brevistipitulatis, 4.5 cm longis, 1 cm latis, acuminatis, basi truncatis, majoribus fere $\frac{1}{2}$ ad costam pinnatifidis, costis nudis atropurpureis, lobis proximis, obliquis, subacutis, ca. 2.5 mm latis, obscure crenulatis, subcoriaceis, inferne pallidis; venis utroque latere ca. 3, obliquis, simplicibus; pinna fertile angustiore, pinnulis 20 ad 25 mm longis, vix 5 mm latis, crenatis; soris contiguis, nudis.

Mount Kinabalu, Gurulau Spur, Topping 1824.

In the small group with distinct fertile and sterile fronds or pinnae; distinguished from *Cyathea dimorpha* (Christ) by having the fertile pinnules less cut than the sterile; and from *C. Hewittii* Copel. by the much smaller and more numerous lobes of the sterile pinnules; much less obviously related to *C. glabra* than is *C. Hewittii*.

CYATHEA ELLIPTICA sp. nov.

Adsunt basis et pars apicalis frondis; rhachi deorsum atrofusca, 6 mm crassa, superne piloso-velutina, ibidem et praecipue

ad latere paleis atrocastaneis squarrosis 5 ad 7 mm longis lanceolatis subulatis integris rigidulis dense vestita, inferne pilis caducis vestita, tum demum verruculosa, sursum rhachibusque pinnarum pallidioribus, superne setosis, alibi glabris; pinnis infimis horizontalibus, subsessilibus, vix 20 cm longis, 5 cm latis; pinnulis 2.5 ad 3 cm longis, 7 mm latis, obtusis, ellipticis, sessilibus, serratis, infimis minoribus; pinna 40 cm ab apice remota sessile, 30 cm longa, 7.5 cm lata, abrupte acuminata; pinnulis 22-paribus, acutis, 1 cm latis, $\frac{1}{2}$ ad costam lobatis, lobis 2 ad 3 mm latis, obliquis, costis superne deorsum sparse et minute pilosis, inferne paleis fulvis parvis et paucis plerisque bullatis deciduis vestitis, lamina glabra papyracea; venulis ca. 3-paribus, simplicibus; soris ferrugineis, exindusiatis, medio inter costam et marginem saepe confluentibus.

Mount Kinabalu, Gurulau Spur, Mrs. Clemens 10859.

This is like the *Alsophila Burbridgei* of Hose and of Christ in having a dense fringe of brown scales on the stipe and lower part of the rachis and is perhaps identical with Hose's plant, at least. Baker described as *Cyathea Burbridgei* a plant without scales and the costae strongly ciliate beneath; the costae of *C. elliptica* are not in the least so. The pinnules are usually abruptly but not greatly dilated at the base.

CYATHEA MOLLIS sp. nov.

Caudice (teste Mrs. Clemens) 1 m alto; stipite 50 cm alto ferrugineo-castaneo, ad pedem paleis fulvis et stramineis linearibus sursum minute serrulatis 1.5 ad 2 cm longis dense immerso, sursum rhachique superne piloso-velutinis, inferne glabrescentibus; fronde 80 cm alta, ovata, longe acuminata, tripinnatifida; pinnis infimis reductis, inframedialibus maximis, subsessilibus, 30 cm longis, 7 cm latis, sensim acuminatis, rhachi superne adpresso-setosa, alibi pilis pallidis 2 ad 3 mm longis vestita; pinnulis multis, fere contiguis, sessilibus, 3 ad 4 cm longis, 1 cm latis, acutis, $\frac{1}{2}$ ad costam pinnatifidis, herbaceis, utraque facie viridibus, costa superne sparse setosa, inferne paleis sparsis minutis plerisque bullatis et subulatis fulvis, et inter eas pilis sparsissimis vestita, costula quaque 1 ad 3 squamulis ornata; lobis ca. 4 mm longis, 3 mm latis, obliquis, obtusis, fere integris; venis utroque latere ca. 4, simplicibus; soris medialibus, minutis, exindusiatis.

Sandakan, Mrs. Clemens 9440.

CYATHEA KEMBERANGANA sp. nov.

Caudice et parte basale stipitis ignotis; fronde 75 cm alta, deltoidea, acuminata; rhachi fusca, superne velutina, alibi glabrescente; pinnis infimis 40 cm longis cum stipitula 3 cm longa,

remotis; pinnulis inferioribus 7 cm longis, 15 mm latis, subobtusis, basi truncatis vel subcordatis, $\frac{2}{3}$ ad costam pinnatifidis, stipitulis earum 5 mm longis, costis superne nigro-velutinis, inferne venisque majoribus paleis lanceolatis vel ovatis 0.5 ad 1 mm longis atropurpureo-setoso-ciliatis deciduis vestitis, atropurpureis; segmentis proximis, superne vernicoso-nitidis, inferne olivaceis; venis utroque latere ca. 5, simplicibus, rectis, infima inferiore remota e costa emissa; soris medialibus, 1 mm latis, sporangiis pilis brevibus brunneis interspersis, indusio nullo vel invisio.

Mount Kinabalu, Kemberanga, Mrs. Clemens 10500.

Probably a near relative of *Cyathea Ridleyi* (Baker), but with lighter axes and stalked pinnules. *C. squamulata* has much more ample fronds, thin in texture, with long, whitish hairs in the sori. *C. recommutata* has dark-purple axes, and less lobed, subdimorphous pinnules.

CYATHEA PALEACEA sp. nov.

Arbor (teste Mrs. Clemens), caudice ut videtur 3 cm crasso apice basibus stipitum paleisque dense immerso; stipite 20 ad 30 cm alto, rhachique ubique densissime paleaceis, paleis pedem stipitis versus 1 cm longis linearibus rigidis atro-castaneo-fuscis integris, ad rhachin et costas inferne pallidioribus laceratis et pilis interspersis praecipue ad costas diversis, superne cum pilis intergradientibus; fronde ca. 50 cm alta, 15 cm lata, acuminata, bipinnata, apice pinnatifida; pinnis infimis deflexis; medialibus, rectis, sessilibus, subacuminatis, 2 cm latis; pinnulis proximis, sessilibus vel plerisque adnatis, obtusis, integris, margine deflexis, rigide coriaceis, costis pallidis superne prominentibus pilis albis longis flaccidis deciduis ornatis, inferne apud rhachin pinnae paleatis, alibi pilis vel squamulis minutis albis appressis ornatis, lamina superne atro-viride, inferne pallidior; venis usque ad 11-paribus, apud costam furcatis; soris magnis, costalibus, globosis; indusio fusco, persistente, poro aperto, demum in fragmenta pauca fisso.

Mount Kinabalu, Paka Cave, Mrs. Clemens 10726 (type), Topping 1669.

Very distinct from any species hitherto known to me, nearest perhaps to *Cyathea dulitensis* Baker, from which it is distinguished by its extreme scaliness. By description it might seem nearly related to *C. philippinensis* Baker, but I believe there is no near affinity between the two.

CYATHEA RIGIDA sp. nov.

C. paleaceae affinis, rhachibus etenim densius paleatis, tota fronde majore et crassiore, paleis basalibus lanceolato-ovatis in vetustate eroso-ciliatis, infimis remotis et reductis, pinnis erecto-patentibus, 17 cm longis, 5 cm latis, pinnulis 25 mm longis, 5 mm latis, majoribus medio ad costam lobatis, lobis triangular-

ibus, lamina et costis superne nigris; aliter vix *C. paleacea* distinguenda.

Mount Kinabalu, Paka Cave, *Topping 1758*.

Very distinct in characteristics available for description, but still very possibly a much more ample form of *Cyathea paleacea*. Judging by the material in hand it seems best to regard them as distinct species. *C. Havilandii* Baker is described as subcoriaceous with the lowest pinnae not reduced, and the veinlets simple.

CYATHEA LONGIPES sp. nov.

Adsunt partes mediales et verosimiliter basales frondis; rhachi castanea, superne minute fusco-furfuracea, alibi glabra, inerme; pinnis longissime stipitulatis, usque ad 45 cm longis, 18 cm latis, acuminatis, rhachi superne fusco-pilosa, inferne deorsum nuda, sursum ut costae sed sparsius paleatis; pinnulis stipitulatis, remotis, usque ad 10 cm longis, 2 cm latis, valde acuminatis, basi rotundato-truncatis, fere ad costam pinnatifidis, costa superne minute pilosa, inferne paleis 1 ad 1.5 mm longis ovatis irregularibus fusco-cinereis subpersistentibus haud dense vestita; segmentis proximis, 10 ad 13 mm longis, 4 mm latis, obliquis, subfalcatis, obtusis, serratis, papyraceis vel subcoriaceis, inferne pallidis, costula superne prominente glabra, inferne deorsum sparse paleata, alibi glabra; venis utroque latere usque ad 8 quarum 5- vel 6-furcatis et his plerisque soriferis; soris infra-medialibus, vix 1 mm latis, castaneis, indusio tenue mox fisso.

Mount Kinabalu, Maraiparai Spur, *Mrs. Clemens 10915* (type), *Topping 1850*. Mrs. Clemens's field note states "trunk 3 ft.—frond 10-15 ft." Well marked by the pedicels, those of the pinnae in hand reaching a length of 8 cm, and of the pinnules, 6 mm.

CYATHEA MEGALOSORA sp. nov.

Stipite 45 cm alto, castaneo, deorsum paleis pallide stramineis linearibus 3 cm longis dense vestito, sursum paleis minoribus sparsius vestito et ob baseos nigros irregularies paelearum deciduarum aspero; rhachi fusca, superne velutina, alibi minute et sparse verruculosa, paleis cinereis sinuosis vestita; pinnis infimis ut videtur maximis, 35 cm longis, 14 cm latis, acuminatis, brevi-stipitulatis, basin versus subangustatis, bipinnatis, rhachi superne dense hirsuta, inferne paleis cinereis linearibus sinuosis 1.5 ad 3 mm longis appressis cum minoribus interspersis densissime vestita; pinnulis utroque latere ca. 20, subsessilibus, vix 12 mm latis, basin versus pinnatis, sursum pinnatifidis, rhachi ut rhachis pinnae vestita: pinnulis II infimis liberis, sessilibus, oblongis, obtusis, 3 mm latis, sequentibus conformibus adnatis margine deflexis, coriaceis, superne nigris, ad costas et venas sparse pilosis, inferne pallidioribus, costis deorsum dense paleatis,

sursum venisque paleis parvis in pila decrescentibus sparse vestitis; venis ca. 5-paribus, plerisque furcatis; soris medialibus, magnis, laminam totam complentibus; indusio laete fusco, mox fisso, persistente; receptaculo parvo.

Mount Kinabalu, Paka Cave to Lobang, *Topping 1759*.

Cyathea crinita (Hooker) Copel., reported by Miss Gibbs, is less densely paleaceous and has narrower ultimate divisions, beside being exindusiate. The scales of *C. megalosora* are typically entire, but those of the upper axes are soft and flexuous, forming thick mats.

DRYOPTERIS Adanson

DRYOPTERIS INCONSPICUA sp. nov.

Lastraea; rhizomate repente vel suberecto, breve, ca. 4 mm crasso, paleis parvis ovatis apiculatis fuscis sordidis vestito; stipitibus confertis, 15 ad 20 cm usque ad pinnae normales altis, fusco-stramineis, deorsum sparse paleatis, sursum rhachique superne velutinis, inferne glabrescentibus, pinnis subnormales 2- ad 4-paribus remotis ad auriculas reductis ornatis; fronde 25 ad 30 cm alta, 8 ad 12 cm lata, acuminata; pinnis infimis normalibus plerumque deflexis et rhachin versus angustatis; medialibus sessilibus vel brevi-stipitulatis, falcato-acuminatis, basi truncatis, 12 ad 16 mm latis, ad alam 1.5 mm latam costalem pinnatifidis, herbaceis, pilis pallidis minutis dense adpressis vestitis; segmentis obliquis, obtusis, 2 ad 3 mm latis; venis utroque latere ca. 4, simplicibus; soris medialibus; indusio fusco, tenue, nudo.

Mount Kinabalu, Kiau, *Topping 1543* (type); Gurulau Spur, *Topping 1837, 1839*.

Apparently a quite distinct species, characterized by the dwarfed lowest pinnae and peculiar pubescence of costae and veins; but without any one distinctive feature to invite attention in the field.

DRYOPTERIS KINABALUENSIS sp. nov.

Lastraea; rhizomate breve, suberecto, paleis nigris lanceolatis valde acuminatis ca. 6 mm longis vestito; stipitibus confertis, 10 ad 17 cm altis, deorsum paleatis atris vel atropurpureis, sursum glabrescentibus et viridescentibus; fronde usque ad 25 cm alta et 8 cm lata, acuminata, rhachi costisque ubique sed praecipue superne brevissime hirsutis; pinnis liberis utroque latere 15 ad 23, infimis haud brevioribus, paullo deflexis, brevissime stipitulatis, aliis sessilibus, inframedialibus horizontalibus, rhachin versus interdum paullo angustatis deinde truncatis, profunde pinnatifidis, tenuiter chartaceis, superne atroviridibus, punctulis minutissimis albis ornatis, nec carent inferne punctulae; segmentis 2 mm latis, obtusis, decidue ciliatis; venulis ca. 5-paribus, simplicibus; soris medialibus, indusio pallido, tenue.

Mount Kinabalu, Paka Cave, *Topping 1719*.

This is from the same place as *Dryopteris gymnopoda* (Baker) C. Chr. and is certainly much like it; but that species is described as smaller, but with the pinnae cut quite to the costa, and with one sorus on each side at the base of each segment; the latter feature might be expected on occasional young plants of *D. kinabaluense*, but such plants are not likely to be more deeply cut than larger ones.

DRYOPTERIS LINEARIS sp. nov.

Lastraea; rhizomate suberecto, 5 ad 10 mm crasso, lignoso, breve, paleis castaneis lanceolatis acuminatis 1 cm longis dense vestito; stipitibus 30 ad 45 cm altis, atropurpureis, nitidis, deorsum paleis paucis ornatis; fronde usque ad 50 cm alta et 8 cm lata, acuta, rhachi atropurpurea superne velutina, inferne nitida; pinnis infimis subremotis vix brevioribus, utroque latere 25 ad 35, brevistipitulatis, 35 ad 45 mm longis, 10 ad 15 mm latis, e basi dilatato sensim angustatis, acuminatis, profunde pinnatifidis, costa superne velutina, aliter glabris, coriaceis, inferne pallidis; segmentis proximis, obtusis, majoribus crenatis vel subserratis; venulis utroque latere ca. 5, simplicibus vel infimis in sementis maximis furcatis; soris superioribus in segmento quoque costularibus, inferioribus divergentibus; indusiis magnis, persistentibus, fulvis, interdum inaequalibus (athyrioideis), nudis.

Mount Kinabalu, Maraiparai Spur, *Mrs. Clemens 11069* (type), 11067.

There is little choice as to whether this should be called *Dryopteris* or *Athyrium*. The conspicuous dark-purple stipes and rachises are duplicated by some similar and probably related species in each genus. I have given this a name in *Dryopteris* because most of the sori are roundish and it is not more nearly related to species known to me in *Athyrium*.

DRYOPTERIS TOPPINGII sp. nov.

Nephrodium, *D. extensae* (Bl.) O. K. affinis, pinnis stipitulatis rhachin versus decrescentibus, adspectu *D. syrmaticae*; rhizomate invisio sed de forma pedis stipitis verosimiliter late repente; stipite 50 cm alta, ad pedem paleis fusco-castaneis linearibus 1 cm longis vestito, sursum rhachique minute griseo-velutinis; fronde ca. 75 cm alta, fere 40 cm lata; pinnis rectis, late linearibus, inferioribus remotis non abbreviatis, stipitulatis, et ad rhachin pseudoarticulatis, ca. 20 cm longis, 3.5 latis, acuminatis, medio ad costam pinnatifidis; segmentis proximis, subfalcatis, obtusis, 5 ad 7 mm latis, pinnularum inferiorum infimis valde reductis, pilis pallidis appressis ciliatis, costis et sparsius venis superne velutinis, inferne minute adpresso-pubescentibus, lamina nuda papyracea; venulis ca. 14-paribus, quarum 3 vel 4

anastomosantibus; soris submarginalibus, contiguis, indusio glabro.

Mount Kinabalu, Lobang, *Topping 1766*.

As is true of *Dryopteris extensa*, the position of the sori is sometimes evident on the upper surface.

DRYOPTERIS LITHOPHYLLA sp. nov.

D. alpestris gregis *D. cucullata*, robustior, rigide coriacea, glabra; rhizomate ut videtur brevi-repente, 5 mm crasso; stipitibus approximatis, validis, 20 ad 25 cm altis, lignosis, basi atropurpureis, sursum fusco-stramineis, glabris, ubique pseudopinnis usque ad tuberculas abrupte reductis donatis; fronde 25 ad 30 cm alto, ca. 10 cm lata, acuminata, rhachi et costis superne velutinis exceptis glaberrima; pinnis proximis, subsessilibus subfalcatis, erecto-patentibus, usque ad 8 cm longis et 15 mm latis, acuminatis, basin versus infimis angustatis, aliis truncatis, profunde dentatis, dentibus oblique deltoideis, acutis; venis conspicuis, ca. 10-paribus quarum 4 anastomosantibus; soris medialibus, indusio parvo glabro, fusco.

Mount Kinabalu, Maraiparai Spur, *Topping 1850*½.

Like *Gleichenia crassifolia* in texture.

MESOCHLAENA R. Brown

MESOCHLAENA TOPPINGII sp. nov.

M. polycarpae similis, pilis rhachidis longioribus et pinnis inferioribus triangulari-hastatis imbricatis distincta; stipite usque ad pinnas infimas reductas 5 cm alto, paleis pilosis linearibus fuscis 10 ad 15 mm longis vestito; parte inferiore frondis lineare, 35 ad 55 cm alto, pinnis ibidem hastato-triangularibus, sursum 2 cm longis, 2.5 cm latis lobis lateralibus recurvatis, late imbricatis; fronde vera 45 ad 60 cm alto, 25 ad 30 cm lata, pinnata, rhachi pilis albis 1.5 vel 2 ad 2.5 mm longis vestita; pinnis fere horizontalibus, sessilibus, 12 ad 15 cm longis, sterilibus 2 cm, fertilibus 10 ad 15 mm latis, acuminatis, basi subhastato-truncatis, ad mediam laminam pinnatilobatis lobis obtusis, lamina papyracea, superne ad costas subadpresso-pilosis, ad venulas pilis sparsis longis ornatis, inter venulas nudis, inferne costis venis et venulis pilosis, lamina inter venulas glandulifera; venulis ca. 9, quarum 2 vel 3 anastomosantibus; indusio elliptico, praecipue ad lineam medialem obscuram dense minute piloso, marginem versus pallido, ad marginem ipsum densissime glandulis minutis obsito.

Kinabalu neighborhood, between Keung and Kibayo, *Topping 1902*.

Mesochlaena polycarpa has a much less conspicuous development of the

reduced lower pinnae, shorter hairs on the rachis, decidedly finer and closer pubescence on the nether surface, and less ornate indusia.

Mr. Topping remarks that he regards this as the most strikingly beautiful fern he has collected.

TECTARIA Cavanilles

TECTARIA MURUDENSIS sp. nov.

Sagenia, Nephrodio ternato Baker, Syn. Fil. 296, affinis, in alas pinnarum glandulifera; rhizomate repente, 5 mm crasso; stipite 35 ad 40 cm alto, fusco, deorsum sordide adpresso-paleato, sursum frondeque glabris; fronde ternata, pinnis elliptico-lanceolatis, valde caudatis, integris; pinna apicale stipitata, usque ad 30 cm longa et 8 cm lata, basi cuneata; pinnis lateralibus sessilibus, paullo minoribus, subcultratis, ad pedem quaeque glandula squamulosa conspicua praditis, papyraceis; venis conspicuis, patentibus, marginem fere attingentibus et ibidem curvatis; soris plerisque apud venis seriatis, nec carent alii irregulariter adpersi; indusio sat persistente, reniforme, lobis interdum imbricatis, parvo.

Sarawak, foot of Mount Murud, native collector 2905 (type), 2945 (Bur. Sci.).

This differs from *Tectaria ternata*, of which I have an apparently typical specimen, in color of stipe and veins, rather firmer texture, more divergent veins, cuneate base of central segment, and in the conspicuous "glands." The latter probably are very dwarfed buds, and suggest affinity to proliferous species. They are uniform on the three fronds in hand. *T. subcaudata* (v. A. v. R.) is described as having a distinctly different rhizome, and fugacious indusia.

ATHYRIUM Roth

ATHYRIUM CLEMENSIAE sp. nov.

A. gregis *A. nigripedis*, *A. Sarasinorum* et *A. philippinensi* simile, quibus praecipue fronde compacta pinnis imbricatis stipite rhachique carnosius distinctum; caudice breve, suberecto, valido, radicibus paleisque immerso, paleis badiis vel castaneis, linearibus; stipite plantae typicalis alpestris 5 ad 8 cm alto, ad pedem dense paleato, alibi paleis angustis ca. 5 mm longis sparsis ornato, sursum glabrescente; fronde ovata, 5 ad 8 cm alta, bipinnata; pinnis brevi-stipitatis, anguste ovatis, obtusis, utroque latere 7 ad 10, deorsum accrescentibus; pinnulis paucis, oblongis vel ellipticis, obtusis, infimis stipitulatis incisis, plerisque confluentibus, crenatis; soris lineari-oblongis, vel late oblongis; indusiis asplenioideis rarius forma typica *Athyrii*, interdum diplazioideis vel reniformibus, neque carent indusia formis aliis, e. g., *Acrophori* et *Leucostegiae*.

Mount Kinabalu, summit of Low's Peak, in rock crannies, *Mrs. Clemens* No. 10621, November, 1915.

The diagnosis just given applies to the form at greatest altitude, where the general appearance seems to be fairly fixed. With decrease of altitude and exposure the fern of course grows more freely, down to its lower limit, which, so far as our collections show, is about the Paka Cave. *Topping's* No. 1698, from between the cave and the summit, has some stunted fronds, but also some 15 cm high and equally wide. His No. 1705 from the immediate vicinity of the cave, has the tripinnatifid fronds ovate and 20 to 25 cm high, with much the aspect of *A. nigripes*, but still with brown, not very dark scales, and the stipe still somewhat fleshy.

Euathyrium reaches its best development in species in the extra-tropical Orient; but within the tropics, each mountain of sufficient height has a group of apparently and probably local species. In this group we have now one species from two Celebes peaks, this one of Kinabalu, and one from Mount Data, Luzon. A somewhat different line of evolution from the same near parent stock is represented on Data, Kinabalu, and the Pangeranggo.

ATHYRIUM ATROPURPUREUM sp. nov.

A. gregis *A. Filix-foeminae*, *A. drepanopteronti* similis, eo paleis, stipitibus et pube atro-purpureiscentibus, lamina tenuiore distinctum; rhizomate suberecto; stipitibus confertis, plerisque atropurpureis, aliis pallidioribus, ca. 20 cm altis, pedibus paleis lanceolatis acuminatis 5 mm longis sparse vestitis, sursum relictis palearum minutarum asperulis; fronde 20 ad 25 cm alta, lanceolata, acuminata, deorsum non angustata, tripinnatifida; pinnis majoribus 5 cm longis, 20 ad 25 mm latis, deltoideo-lanceolatis, acuminatis, brevipedicellatis, rhachibus sursum vel ubique alatis; pinnulis sessilibus vel adnatis, oblongis, pinnatifidis vel sursum dentatis; segmentis acutis, integris vel furcatis; lamina papyracea vel chartacea, superne pilis et squamulis minutis deciduis sparse vestita, obscura; venis nigris; soro in segmento quoque uno, laminam ejus fere complente; indusiis polymorphis, plerisque dryopteroides, aliis (parvis) forma *Leucostegiae*, aliis athyrioideis.

Mount Kinabalu, Low's Peak, *Mrs. Clemens* 10620, *Topping* 1696.

ATHYRIUM ATROSQUAMOSUM sp. nov.

Diplazium, *A. Blumei* affine, soris brevibus, lamina tenuiore, stipite deorsum paleis angustissimis nigris nitidis asperis subcrinitis 5 ad 12 mm longis dense vestito; stipite 40 cm alto, deorsum nigro sursum sordide brunneo-stramineo; rhachibus in sulcis dorsalibus pilosis, alibi paleis paucis parvis irregularibus deciduis ornatis; fronde 1 m alta, 60 cm lata, triangulari; pinnis sat remotis, stipitatis, acuminatis, infimis 35 cm longis; pinnulis

multis, stipitulatis, inferioribus et submedialibus ca. 12 cm longis, 15 mm latis, valde acuminatis, basi truncatis, fere ad costam nigram pinnatifidis, segmentis 3 ad 4 mm latis, oblongis, obtusis, serrato-dentatis; venis fere omnibus simplicibus; lamina papyracea, inferne subpallidior glabra; soro infimo solummodo saepe diplazioideo; soris costularibus, brevibus, indusio laete brunneo.

Mount Kinabalu, Maraiparai Spur, *Mrs. Clemens 11051*.

This fern has the remarkable coat of absolutely black scales, completely clothing the apex of rhizome and base of stipe, characteristic of *Athyrium meyenianum*; in other respects it is much like *A. Blumei*, except in the details noted above.

POLYPODIUM Linnaeus

POLYPODIUM KINABALUENSE sp. nov.

Grammitis minuta, rhizomate erecto, apice paleis pallidis minutis lanceolatis vestito; stipitibus permultis confertis, usque ad 5 cm longis castaneis, glabris, erectis; frondibus lineari-oblan-
ceolatis, 3 ad 5 cm altis, 2.5 ad 4 mm latis, obtusis, deorsum sensim angustatis, glabris, tenuiter coriaceis; venis furcatis ramis subaequalibus, ramo superiore apud furcam sorifero; soris superficialibus vel levissime immeris, vix elongatis.

Mount Kinabalu, altitude 3,700 meters, *Mrs. Clemens 10649* (type), 10618 partim.

A very distinct little fern of the Alpine summit. Mixed with *No. 10649* is one small plant which may be a *Scleroglossum*.

POLYPODIUM BROOKSII sp. nov.

Polypodium hirtellum Brooks in Sarawak Mus. Journ. 1 (1912) 49, non Blume.

Grammitis, rhizomate suberecto, paleis pallide brunneis ovatis obtusis vel acutis vestito; stipitibus confertis, haud articulatis, filiformibus, 0.5 ad 1 cm longis, pilis vinicoloribus 1 ad 2 mm longis ornatis; fronde 4 ad 7 cm alta, plerumque ca. 3 mm, rarius usque ad 5 mm lata, obtusa vel subacuta, deorsum sensim angustata, integra, subcoriacea, ubique setosa, setis usque ad 3 mm longis, rubidis; venis sterilibus plerisque simplicibus, fertilibus prope costam furcatis, soro orbiculare ramum superiorem brevissimum insidenti et complente, receptaculo subelongato.

Sarawak, Mount Bongo, *Brooks*, February, 1908.

So far as one might judge from diagnoses, this might be *Polypodium lasiosorum* Hooker; but study of Javan material satisfies me, as it has Blume, Beddome, and others, that the latter is only a small form of *P. hirtellum* Bl., with forks of the veins subequal. I have never seen *P. hirtellum* except in Javan material. Beddome, *Ferns of British India* 172, 212, twice figures a Ceylon fern, probably similar in venation to that described here, although he describes the veins on page 172 as simple; we have this

fern in Luzon and have called it *P. hirtellum* in error. I now believe it to be *P. Reinwardtii*. *Grammitis nana* Fée is also described as having simple veins; whatever it is, the name cannot be transferred to *Polypodium*. As to the venation of *P. lasiosorum*, van Alderwerelt, Malayan Ferns 580, says "veins not discernible,"—which may depend on how it is examined.

My specimens of *Polypodium Brooksii* are somewhat old and the sporangia seem to be naked; those of *P. Reinwardtii* and *P. hirtellum* bear a few setae.

POLYPODIUM CALCIPUNCTATUM sp. nov.

Grammitis *P. Frederici et Pauli* Christ affinis, subglabra et punctulis calcareis ornata; rhizomate erecto, paleis lanceolatis fulvis dense ciliatis vestito; stipitibus confertis, 3 ad 4 cm longis, gracilibus, pilis 2 ad 2.5 mm longis pallidis et rubis vestitis; fronde pendente, usque ad 25 cm longa, ca. 13 mm lata, linguiforme, subacuta, deorsum angustata, integra vel rarius obscure et late crenulata, crassa, superne glabrescente et ad apices venularum albo-punctata, inferne sparse pilosa; venis utrinque pinnatis, immersis; soris irregulariter a costa fere ad marginem adpersis, superficialibus, orbicularibus, inter sporangia pilis paucis.

Mount Kinabalu, Kemberanga, Mrs. Clemens 10530.

While near to *Polypodium Frederici et Pauli* of Celebes, this fern has a narrower frond, with parallel sides and the form of a narrow *P. setigerum*, less conspicuous and almost naked costa, and thicker texture.

POLYPODIUM MULTISORUM sp. nov.

Grammitis, praecedente (*P. calcipunctato*) affinis; rhizomate breve, suberecto, radicibus et sursum basibus stipitum omnino oblecto, paleis veris ob dissectionem ipsarum in pilos minutos pallidos carentibus; stipitibus multis confertis, 2 ad 4 cm longis, filiformibus, pilis pallidis usque ad 2 mm longis densissime hirsutis; fronde ca. 15 cm longa, 8 ad 12 mm lata, utrinque angustata, subacuta, integra vel saepius late crenata, subcoriacea, superne glabrescente, inferne ubique pilosa; venis sinuatis, irregulariter utrinque pinnatis; soris irregulariter adpersis vel sub-3- vel 4- seriatis, oblongis, densissime pilosis, superficialibus.

Mount Kinabalu, Paka Cave, Topping 1665 (type) 1668, 1682, 1711. No. 1682 is immature and might be confused with other species.

While more like *Polypodium Frederici et Pauli* in form and texture, this fern is clearly distinguished by the elongate sori, which remain clearly marked by dense tufts of hairs, after the sporangia are removed.

POLYPODIUM MURUDENSE sp. nov.

Eupolypodium pinnatifidum anguste lineare; "rhizomate" erecto, breve, paleis ovato-lanceolatis brunneis inter stipites vestito; stipitibus confertissimis, ca. 2 mm altis, vel 1 cm altis et sursum alatis, pilis paucis albidis ornatis, mox glabrescentibus; fronde 6 ad 9 cm alta, 2.5 mm lata, in dentes triangulares obtusos

-pinnatifida, in vernatione pilis brevissimis albidis vestita, glabrescente, papyracea, sinubus inter dentes dentibus ipsis reversis aequalibus; vena in dente quoque una, simplice, soro tantum uno, inframediale, subsuperficiale.

Mount Murud, native collector, 2924 (Bur. Sci.), December, 1914.

Nearer to *Polypodium subpinnatifidum* than to *P. alternidens*; differing from the former in having almost sessile, narrower fronds and triangular, not rounded, segments; from the latter in the closer teeth and thinner texture.

POLYPODIUM BRACHYPODIUM sp. nov.

Species *P. colorato* Copel. similis et affinis, paleis mollioribus integris distincta; rhizomate 3 ad 4 mm crasso, calcareo, paleis rufo-castaneis peltatis sensim in caudam angustatis 5 mm longis integris mollibus vestito; phyllopodiis brevissimis; stipitibus inter se ca. 4 mm distantibus, 10 ad 18 cm altis, glabris, atrofusciis vel (frondium juvenalium) stramineo-fusciis; fronde usque ad 30 cm alta et 7 cm lata, acuminata, pectinata, vix deorsum angustata, rhachi atro-fusca, nuda; segmentis utroque latere usque ad 60, fere horizontalibus, 3 ad 4 mm latis, acutis, apices versus serrulatis, ala angusta confluentibus, papyraceis vel subchartaceis, opacis, infimis decurrentibus; venis deorsum seriem unam areolarum includentibus, aliter liberis, furcatis, venis inclusis nullis, apices versus segmentorum liberis, furcatis, tum demum simplicibus; soris ad ramos inferiores acroscopicos venarum, costae quam margini propioribus, superficialibus, parvis, utroque latere costae usque ad 18.

Mount Kinabalu, Gurulau Spur, Topping 1823 (type), 1620; Lobang, Mrs. Clemens 10354; Kiao, Mrs. Clemens 10225.

Very similar in appearance to *Polypodium coloratum*, but larger than any known specimens of the latter, with closer fronds, and distinctly different paleae; the costae of the segments are straight in *P. brachypodium*, but wavy above the middle in the type of *P. coloratum*.

Polypodium cesatianum Baker is probably a fern of this most interesting Bornean group, as is certainly true of the fern described under that name, as a *Eu-polypodium*, by van Alderwerelt, Malayan Ferns, 603. In my judgment, this name is without standing in systematic botany. Baker published it without a diagnosis, merely stating that Beccari's plant, *P. papillosum* Cesati, non Blume, was a distinct species. Cesati suggests differences from true *P. papillosum*, by saying that such may be due to the state of development of his very small specimen; but all he tells about it is that it agrees with *P. papillosum* in not having the lower pinnae reduced—which certainly is no diagnosis. Beccari and Christ merely list the plant; and the first description, based on a collection by Hallier instead of on the original, was published by van Alderwerelt, in *English and in 1909*.

Judging by place of collection, Beccari's plant is likely to be *P. coloratum* Copel., 1908, which I published without suspecting that I might have *P. cesa-*

tianum, supposed at that time to have free veins. *P. cesatianum* is described by van Alderwerelt as having brown paleae and the margin "slightly, not regularly crenate;" it may be *P. coloratum* or may not; at any rate, the two are closely related. If *P. cesatianum* Baker is neither *P. coloratum* nor the plant collected by Hallier, it still awaits description. If all three are distinct, some good botanical lawyer should decide what plant should be called *P. cesatianum*. Was the type collected by Beccari or by Hallier? Has a *nomen nudum*,—such as *P. cesatianum* was before 1909, and under our strictest rules still is—and, as such, invalid, a type valid enough to fix the application of the name? Or could van Alderwerelt, intentionally or inadvertently, choose a new type specimen to go with Baker's name? Is it *P. cesatianum* Baker or *P. cesatianum* v. A. v. R.?

POLYPODIUM OCCULTIVENIUM sp. nov.

Species *P. rupestri* Bl. affinis; rhizomate repente, paleis rufo-brunneis peltatis sub insertione non protractis supra basin anguste lanceolatis apicibus longis setiformibus dense vestito; stipitibus approximatis, frondum sterilium ca. 4 cm, fr. fertilium ca. 10 cm altis, fusco-stramineis, nudis, rectis; fronde sterile 13 ad 16 cm longa, 2.5 ad 3.5 cm lata, lineari-elliptica, integra, coriacea, glabra, apice rotundata, basi acuta; costa inferne prominente, venis inconspicuis; fronde fertile paulo longiore; soris inter venas biseriatis, multis, superficialibus.

Sarawak, Bidi, Brooks, May, 1909.

Polypodium rupestre Bl. differs from this in having darker, less dense, and less setiform paleae, acuminate fronds broadest near the base, and more rigid texture.

POLYPODIUM ALBIDO-PALEATUM sp. nov.

Species *P. triquetrum* Bl. affinis; rhizomate repente, nigro, rugoso, 4 mm crasso, paleis ochroleucis vel albidis peltatis et sub insertione protractis anguste ovatis apicibus acuminatis deciduis donatis tum demum omnino deciduis vestito; stipitibus remotis, fuscis vel atro-fuscis, validis, 7 ad 12 cm altis; fronde 25 ad 40 cm alta, 7 ad 8 cm lata, elliptico-lanceolata, abrupte brevi-acuminata, basi rotundata vel subcuneata, integra vel apicem versus subserrulata, rigide coriacea, glabra; costa et venis primariis praestantibus; soris parvis, inter venas biseriatis vel subirregulariter adspersis inter costam et marginem usque ad 18, superficialibus.

Mount Kinabalu, Paka Cave to Lobang, Topping 1749 (type); Marai-parai Spur, Mrs. Clemens 11060.

Polypodium triquetrum Bl. has larger, darker and more persistent paleae, smaller and distinctly lanceolate fronds and larger and less numerous sori, regularly arranged in double rows. The confusion of *P. triquetrum* and *P. rupestre*, in various compendia, can be due only to failure to observe the paleae.

POLYPODIUM ITHYCARPUM sp. nov.

Species gregis *P. nigrescentis* Bl.; stipite 25 cm alto vel altiore; fronde spectabile ultra 50 cm alta, late ovata, ad alam 5 ad 10 mm latam pinnatifida; segmentis ultra 35 cm longis, 3 ad 5 cm latis, integris, glabris, membranaceis, angulo 45° distantibus, costa valida, plerumque ad basin deflexa; venatione inconspicua; soris utroque latere costam prope uniseriatis, inter se remotis, superne 1 mm elevatis, truncatis, usque ad 3 mm latis.

Mount Kinabalu, Kiau, *Topping* 1578 (type), a small frond; Lobang, *Topping* 1778, a fragment of a large frond.

On the specimens collected, the tips of every segment except one stunted one are broken off in collection or drying; the longest fragment is 35 cm long. In spite of the great size, and the thinness, the venation is no more conspicuous than that of *P. punctatum* (L.) Sw. The plant is further distinguished from *P. nigrescens* and *P. longissimum* (which are not easily distinguished in Borneo) by the even more prominent sori, the distance between them, and their remoteness from the margin.

CYCLOPHORUS Desvaux**CYCLOPHORUS BORNEENSIS** sp. nov.

Nipholobus gregis *C. floccigeri*; rhizomate late repente, 2.5 mm crasso, nigro, dense paleato, palearum basibus peltatis nigris, pallido-marginatis, paleis anguste lanceolatis, castaneis, griseo-marginatis, deinde sursum griseis, longissime attenuatis, rectis vel subcrispis, patentibus, integris; stipitibus remotis, 3 ad 6 cm altis, albo-floccigeris, glabrescentibus; fronde ca. 25 cm alta, 10 ad 12 mm lata, utrinque sensim angustata, coriacea, margine sicco deflexo, superne pilis fulvis longe-stellatis deciduis vestita, nec punctata nec squamulosa, inferne tomento denso et profundo occulta, pilis stellatis saepe seta erecta centrale obscura ornatis, ramis aliis saepius pallidis; venis liberis omnibus excurrentibus, in areola quaeque plerumque 3; soris irregulariter ca. 4-seriatis, laminam totam complentibus, haud ad partem distalem frondis restrictis.

Mount Kinabalu, Kiau, *Topping* 1508.

OREOGRAMMITIS Copeland genus novum

Frondibus confertis, stipitatis, simplicibus, integris, parvis; venis (nisi soriferis) liberis; soro costa parallelo et proximo, lineare, superficiale, nudo; paraphysibus nullis. Genus *Eupolypodio* derivatum.

OREOGRAMMITIS CLEMENSIAE sp. nov.

Rhizomate adscendente, brevissimo, paleis pallido-fuscis lanceolatis vel ovatis acutis 2 ad 3 mm longis dense oblecto; stipitibus

filiformibus, castaneis, 1.0 ad 2.5 cm altis; fronde lineari-oblancoolata, 1.5 ad 3.0 mm lata, 2 ad 3 cm longa, obtusa, deorsum sensim attenuata, subcucullata, subcoriacea, fusca, pilis sparsissimis concoloribus mox deciduis vestita; venis inconspicuis, simplicibus vel furcatis; soris usque ad 12 mm longis, subapicalibus, lateribus frondis deflexis protectis.

Mount Kinabalu, Low's Peak, altitude 3,670 meters, Mrs. Clemens, mixed with No. 10618, the remainder of which is *Polypodium kinabaluense*.

This fern differs from *Scleroglossum* in the very essential feature of its strictly superficial, or even slightly elevated sori. The filamentous stipes, leaving the short rhizome or caudex with a conspicuous covering of paleae, also give it a quite distinct appearance. The protection of the sori by the deflexed sides of the arched apex is mechanically like that already known in the case of *Hymenolepis platyrhynchos*; and in both cases the protection tends to be raised and so to expose the sorus when the frond is dry, but to fold down when it is wet.

In its characters, *Oreogrammitis* stands between *Scleroglossum* and *Polypodium*, and possibly illustrates the origin of the former; but as it is known only from the isolated summit of Kinabalu, it seems more likely that it is an independent offshoot.

SCLEROGLOSSUM van Alderwerelt van Rosenburgh

SCLEROGLOSSUM ANGUSTISSIMUM sp. nov.

Rhizomate suberecto, basibus stipitum, radicibus filiformibus rigidis atrofusis, atque paleis lanceolatis integris pallido-fuscis usque ad 5 mm longis 1 mm latis acutis, densissime oblecto; stipitibus ut placet, aut nullis, aut alatis et 1 ad 4 cm altis, complanatis; fronde lineari-spatulata, parte subapicale fertile 5 ad 10 mm longa, 1.5 mm lata, deorsum ad alam usque ad caudicem protractam stipitis sensim angustata, apice obtusa, coriacea, glabra; costa haud prominente, usque ad apicem attingente; venis brevibus, liberis, immersis; soris intramarginalibus, fere ad costam immersis, sulcis decurrentibus, paraphysibus nullis.

Mount Kinabalu, Marai Parai Spur, Mrs. Clemens 11048. An unmistakable *Scleroglossum*, but with more the form and size of a *Monogramma*. From above Paka Cave, we have a single specimen of another small *Scleroglossum*, mixed with the type collection of *Polypodium kinabaluense*; until more material may be brought in, I am not sure that it is not a dwarfed specimen of *S. pusillum*.

KOORDERSIOCHLOA JAVANICA MERRILL, A NEW GENUS AND
SPECIES OF GRAMINEAE FROM JAVA

By E. D. MERRILL¹

(From the botanical section of the Biological Laboratory, Bureau of Science,
Manila, P. I.)

ONE PLATE

KOORDERSIOCHLOA² Merrill genus novum *Gramineae-Aveneae*.

Spiculae pauciflorae, laxe paniculatae, rhachilla supra glumas inferiores elongata et valde hirsuta; rhachilla inter flores valde elongata et articulata, infra (=rhachilla propia) glaberrima, supra (=callus) hirsuta, floribus inferioribus hermaphroditis, superioribus masculinis; glumae superiores vacuae. Glumae 2 inferiores vacuae, sub articulatione persistentes, inaequales, lanceolatae, acuminatae, obscure carinatae (gluma minor obscure 3-nervia; gluma major distincte 5-nervia, nervis subparallelis). Glumae florentes anguste lanceolatae, submembranaceae, 7-nervae, dorso rotundatae, apice acuminatae et 2-dentatae quam vacuae multo longiores, dorso sub apice arista longa torta tenui haud geniculata instructae. Glumae superiores florem 3 foventes; ultimae valde reductae, ananthae. Palea angusta, 2-carinata, apice obscure 2-dentata. Stamina 3. Ovarium glabrum. Styli breves, distincti, ovarii apice inserti, stigmatibus plumosis. Caryopsis oblonga, glabra, leviter compressa, obscure sulcata, libera, apice appendiculata et stigmatum reliquiis coronata. Gramen elatum foliis planis, habitu *Avenae Junghuhnii* Büse. Ligula elongata. Paniculae ramuli capillares, spiculis longiusculis, nutantibus, glumis imbricatis, florentibus 4 vel 5, superioribus 2 vel 3 valde reductis, vacuis, aristae conjunctim contortae.

KOORDERSIOCHLOA JAVANICA Merrill sp. nov.

Culmo erecto, 1 m alto, basi 2 ad 3 mm diametro, minutissime scaberulo. Foliorum vaginae internodia superantia, striatae, minutissime scabridae; ligula elongata, glabra, fissa, 5 ad 7 mm longa, infra leviter incrassata, supra submembranacea, lobis obtusis, circiter 2 mm latis; lamina anguste lanceolata, attenuato-

¹ Professor of botany, University of the Philippines.

² Nomen e cl. Koorders et *chloa* (χλόα).

acuminata, circiter 15 cm longa et 7 mm lata, membranacea, glabra vel junioribus subtus leviter ciliato-pilosa. Panicula exserta, angusta, laxa, circiter 15 cm longa, glabra, rami pauci, tenues, adscendentes; pedicelli graciles. Spiculae lanceolatae, circiter 2 cm longae (aristis exceptis). Glumae 2 inferiores steriles glabrae, lanceolatae, acuminatae; gluma minor, 8 ad 9 mm longa et 1.2 mm lata, obscure carinata et obscure 3-nervia; gluma major 11 ad 12 mm longa et 1.6 mm lata, distincte 5-nervia. Rhachillae articulis 4 mm longis (rhachilla propria glaberrima, 2 mm longa; callus dense hirsutus, 2 mm longus). Glumae fertiles plerumque 4, 12 ad 14 mm longae et 2.5 mm latae, glabrae, 7-nerviae, apice acuminatae et 2-dentatae, dorso rotundatae, arista tenui, contorta, haud geniculata, 4 cm longa, circiter 3 mm infra apicem inserta; glumae superiores valde reductae, vacuae. Caryopsis anguste oblonga, leviter compressa, glabra, 5 ad 6 mm longa, indistincte sulcata, apice appendiculata et stigmatum reliquis coronata.

Java orientalis, Prov. Besoeki, Idjen Plateau, in sylvis *Casuarinae montanae*, leg. Koorders 408468, alt. 1,800–2,000 m. s. m., July 21, 1916.

A remarkable grass, well characterized by its narrow, lax panicles; its very slender, twisted but not geniculate awns, which are much longer than the spikelets, those of each spikelet closely twisted together; and its elongated rachilla joints. The space between the flowering glumes is about 4 mm, of which 2 mm is the slender, glabrous, rachilla proper, and the other 2 mm the somewhat thickened, prominently hirsute callus. The lower one or two flowers are perfect, the succeeding two or three staminate, while the uppermost two glumes are very greatly reduced, empty, the last one practically reduced to a very slender awn 5 to 6 mm in length which terminates the rachilla.

I was at first disposed to place this apparently undescribed genus in the *Eufestuca*, near the genus *Festuca*, but it is apparently better placed in the *Aveneae*, near the Australian genus *Amphibromus* Nees. It differs from *Amphibromus* in its more numerous nerved empty and flowering glumes, the later toothed, not cleft; its twisted but not geniculate awns; and its caryopsis, which is obscurely sulcate. Regarding the awns of *Amphibromus* Steudel states "valvula inferior * * * infra apicem membranaceum bifidum vel tridenticulatum aristata, arista stricta (siccando ad horizontem reflexa nec geniculata)." Bentham describes the awns as "florentes * * * medio dorso arista torta geniculataque tenui instructae" and in his *Flora Australiensis* as "Flowering glumes * * * with a dorsal twisted and bent awn attached at about the middle."

Australian material representing *Amphibromus neesii* Steud., for which I am indebted to Mr. J. H. Maiden, director of the Botanic Garden, Sydney, N. S. W., and a specimen in the Buitenzorg Herbarium, collected by *Reader*, shows that this genus is radically different from *Koordersiochloa* in many characters, including its much smaller spikelets, the flowering glumes awned from about the middle of the back, the awn prominently geniculate or bent. The awns are, moreover, free and spreading, not twisted together in the manner so characteristic of *Koordersiochloa*. In *Amphibromus* the callus, while prominently bearded, is much shorter than are the joints of the rachilla. The alliance of *Koordersiochloa* with *Amphibromus* was originally determined from the description of the latter genus, and now that specimens are available for purposes of comparison, I am still of the opinion that this is the correct disposition of the new Javan genus.

ILLUSTRATION

PLATE I. *Koordersiochloa javanica* Merrill. Koorders et Mangoendimedjo delin. A, from life; B to N, from herbarium material *Koorders* 40846 β .

- A. Habit sketch of a flowering plant.
- B. Part of a flowering and fruiting plant.
- C. Spikelet in flower.
- D. Flower.
- E. Stamen.
- F. Pollen grain.
- G. Gynaecium.
- H. Fruiting glume and palea, the former with an awn.
- J. Apex of a flowering glume.
- K. Palea.
- L. Caryopsis.
- M. Apex of a caryopsis with the thickened base of the style.
- N. Starch grains.



PLATE I. KOORDERSIOCHLOA JAVANICA MERR.

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